AN ABSTRACT OF THE DISSERTATION OF

Adam S. Hadley for the degree of Doctor of Philosophy in Forest Science presented on August 27, 2012.

Title: Independent Effects of Habitat Loss and Fragmentation on Pollination: Tropical Forest Fragmentation Alters Hummingbird Movements and Pollination Dynamics

Abstract approved:

Matthew G. Betts W. Douglas Robinson

A growing body of work reveals that animal-mediated pollination is negatively affected by anthropogenic disturbance. Landscape-scale disturbance results in two often inter-related processes: (1) habitat loss, and (2) disruptions of habitat configuration (i.e. fragmentation). Understanding the relative effects of such processes is critical in designing effective management strategies to limit pollination and pollinator decline. I reviewed existing published work from 1989 to 2009 and found that only six of 303 studies separated the effects of habitat loss from fragmentation. I provide a synthesis of the current landscape, behavioral, and pollination ecology literature in order to present preliminary multiple working hypotheses to explain how these two landscape processes might independently influence pollination dynamics (Chapter 2). Despite the potential importance of independent effects of habitat fragmentation, effects on pollination remain largely untested. Studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines. I also found that the field of landscape pollination ecology could benefit from quantification of the matrix, landscape functional connectivity, and pollinator movement behavior.

To test the hypothesis that pollinator movement can be influenced by landscape configuration, I translocated radio-tagged hummingbirds across agricultural and forested

landscapes near Las Cruces, Costa Rica (Chapter 3). I found return paths were on average more direct in forested than in agricultural landscapes. In addition, movement paths chosen in agricultural landscapes were more forested than the most direct route suggesting that hummingbirds avoided crossing open areas when possible.

To determine if differences in pollinator movement translated to differences in plant reproduction, I tested the relative importance of landscape composition versus configuration on the reproductive success of *Heliconia tortuosa*, a hummingbird-pollinated forest herb (Chapter 4). I used a stratified random sampling design to select sites across orthogonal gradients in patch size, amount of forest, and elevation. I tested four landscape change hypotheses (i.e., local, landscape composition, landscape fragmentation, and fragmentation threshold). I found that *Heliconia* reproduction supported both the local site and landscape fragmentation hypotheses. Seed set increased with increasing forest patch size independent of amount of forest in the surrounding landscape. I also found that increasing patch size positively influenced the relative abundance of pollinators. The observed differences in seed set likely resulted from differences in hummingbird movements (Chapter 3) and/or abundance under different landscape configurations.

Independent Effects of Habitat Loss and Fragmentation on Pollination: Tropical Forest Fragmentation Alters Hummingbird Movements and Pollination Dynamics

by
Adam S. Hadley

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Adam S. Hadley, Author

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CONTRIBUTION OF AUTHORS

Chapter 2: Dr. Matthew G. Betts provided critical assistance with the formulation of this chapter and input on the writing throughout.

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Chapter 4: Dr. Matthew G. Betts provided assistance with the experimental design, methods and analysis. Dr. Betts also participated in data collection. Sarah J.K. Hadley assisted with data collection and provided input on the analysis and writing. Dr. W. Douglas Robinson assisted with study conceptualization and design. Dr. W. John Kress assisted with experimental methods and provided critical understanding of *Heliconia tortuosa* life history.

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DEDICATION

To teachers and students, may we all strive to do our best as both.

Independent Effects of Habitat Loss and Fragmentation on Pollination: Tropical Forest Fragmentation Alters Hummingbird Movements and Pollination Dynamics

1 GENERAL INTRODUCTION

Landscape changes are often thought to be one of the major threats to biodiversity (Pimm and Raven 2000). With ever expanding human population size and resource needs, anthropogenic transformation of landscapes is only expected to increase (Millennium Ecosystem Assessment 2005). The combined effects of landscape disturbance and other factors such as invasive species and global climate change, present real issues for conservation of biodiversity and ecosystem services. However, understanding the many intricacies of landscape disturbance has, and continues to, pose many problems for landscape and conservation ecologists (Lindenmayer and Fischer 2007).

Landscape structure is defined by two major elements (Turner 1989). Landscape composition is the type and amount of habitat or cover types within a landscape. Habitat loss is the dominant process through which anthropogenic activities alter landscape composition. Therefore, landscape configuration reflects the spatial pattern of landscape elements, while fragmentation *per se* refers to the spatial configuration of remaining habitat, independent of the amount of total habitat within the landscape (Fahrig 2003).

Examining the relative importance of composition and configuration has proved to be problematic. Landscape alteration typically occurs in such a manner that as habitat is lost the remaining landscape also becomes more fragmented, containing smaller and more isolated patches. Therefore, both habitat loss and fragmentation are typically confounded in nature (Fahrig 2003). The relative importance of one process or the other can only be discerned if measures are taken to address this confound by controlling for one process while examining the other. This can be done statistically or experimentally through appropriate study designs. Habitat loss has been shown to have profound negative consequences for biodiversity (Fahrig 2003). Yet despite strong theoretical arguments the empirical support for effects of habitat fragmentation per se is more limited (Prugh et al. 2008). Deciphering the relative importance of landscape fragmentation and habitat loss is crucial for policy makers and landscape planners who need to know which characteristics, such as amount of certain cover types or landscape connectedness, will conserve biodiversity and ecosystem function most effectively (Kremen 2005, Smith et al. 2010).

The majority of plant species depend on animal pollination for sexual reproduction and many ecosystem services such as food production; medicine, carbon sequestration, and flood control are linked to this service (Kremen et al. 2007). However, large-scale parallel declines of plants and pollinators foreshadow that pollination as a critical ecosystem function could be at risk (Biesmeijer et al. 2006). Decreases in pollination and subsequent reduced plant fecundity are considered an early step in the demographic collapse of plant populations (Nason and Hamrick 1997, Aizen et al. 2002). Landscape disturbance is hypothesized to be one of the primary factors behind these widespread pollination declines (Aguilar et al. 2006, Eckert et al. 2010) and this has necessitated a link between the fields of pollination ecology and landscape ecology. The development of this new 'landscape pollination ecology' field has not been without its complications. Despite a great deal of work documenting effects of landscape changes, we still have relatively limited knowledge of the mechanisms behind these differences (Eckert et al. 2010). Very little is known about what components of pollination systems such as plant demography, pollinator density or pollinator movement are most susceptible to disturbance.

The goal of this thesis is to explore independent effects of the two major components of landscape transformation (i.e., changes in composition and configuration) on pollination systems. First, I quantify the degree to which the hypothesis that landscape fragmentation drives pollination declines (Ashworth et al. 2004) has been tested in pollination systems with a detailed literature review. Secondly, I use two field experiments to fill important gaps in our knowledge of apparent landscape-driven pollination declines.

I chose a tropical pollination system since the tropics represent an area of extremely high biodiversity and accelerating landscape transformation. Tropical pollination systems are also relatively underrepresented in existing landscape pollination studies despite showing the highest rates of species loss (da Silva and Tabarelli 2000) and pollen limitation (Vamosi et al. 2006). I focused my research on an understory forest herb, *Heliconia tortuosa* (Red twist), that is pollinated by hummingbirds. The relatively large size of these hummingbirds compared to most pollinators allowed me to capitalize on recent

advancements in miniaturized radio-tags to collect detailed pollinator movement data for this system. I experimentally tested the hypothesis that pollinator movements are altered by landscape disturbance using translocations to measure landscape functional connectivity from the pollinator's perspective (Bélisle 2005). I then used a mensurative experiment test for independent effects of composition and configuration on pollination success in this system.

In order to identify how successful pollination ecologists have been at incorporating concepts from the fields of landscape and behavioral ecology, I examined existing work on landscape change and pollination. In Chapter 2, I provide a synthesis of the current landscape, behavioral, and pollination ecology literature, to present preliminary multiple working hypotheses for explaining how landscape processes might influence pollination dynamics. By highlighting important knowledge gaps and pointing out promising new avenues of research I hope to assist the continued development of landscape pollination ecology.

In Chapter 2 I describe the three main components of pollination systems that can be altered by landscape change (i.e., plant demography, pollinator density, and pollinator behavior; Ghazoul 2005, Kremen 2005) and, when necessary, draw on broader landscape or behavioral ecology work to outline how each of these components might be altered by the independent effects of composition and configuration. I next examined the degree to which the hypothesis that landscape configuration can drive reduced pollination has been tested. I did this by conducting a systematic literature review of studies examining supposed 'fragmentation effects' on pollination and subsequently quantifying the number of studies which have successfully disentangled the confounding effects of composition from configuration.

If the fragmentation hypothesis had been tested, as was implied by the titles of many articles (e.g., "Effects of fragmentation on pollination…"), efforts to advance the field could be better spent in alternative directions. However, if pollination ecology had fallen into the same pitfalls that have plagued landscape ecologists for years (i.e., inability to attribute effects to changes in configuration versus composition; Fahrig 2003,

Lindenmayer and Fischer 2007), then additional studies designed to disentangle these effects are needed. The gaps in existing knowledge outlined in this chapter led to the two main questions that I addressed in the third and fourth chapters of this thesis:

1. How are the movements of pollinators affected by landscape configuration? (Chapter 3)
2. How are the plants that depend on services from these pollinators affected by the independent effects of composition and configuration? (Chapter 4)

Despite the potential for direct effects of animal movement decisions on pollination, the pollinator movement hypothesis has received little attention due to the inherent difficulties in tracking small pollinators (Ghazoul 2005). Consequently, knowledge of pollinator movements has been largely speculative. Experimental manipulations, such as translocations and precise tracking methods, are thought to provide meaningful measures of functional connectivity; the rates and paths of animal return to territorial patches provide measures of landscape resistance (Bélisle 2005). This functional connectivity of a landscape has important implications for pollen flow and subsequent pollination success (Kremen et al. 2007). In Chapter 3, I investigated the effects of tropical forest conversion to agriculture on movements of the Green Hermit (*Phaethornis guy*), a generalist forest hummingbird. I chose a generalist species because resultant changes in its movements will likely have broader ecological impacts than in the case of more specialized pollinators (Olesen et al. 2007). Green Hermits are forest-dependent, but persist in fragmented landscapes (Borgella et al. 2001), making them ideal for comparing movements between altered and intact landscapes. I used experimental translocations to standardize motivation (Bélisle 2005) and compare functional connectivity of disturbed and undisturbed landscapes from the perspective of these pollinators. Having collected detailed information on hummingbird movements in relation to different landscape elements (Chapter 3), I had an opportunity to test how differences in pollinator movement patterns might be reflected in the reproductive success of the plants that depend on them (Chapter 4).

In addition to difficulties in separating effects of composition from those of configuration (discussed in Chapter 2), landscape-scale pollination studies have proved complicated due to issues relating to inadequate replication (Eckert et al. 2010), choice of scale (Brosi et al. 2008), and definitions of habitat or matrix (Jules and Shahani 2003). Most studies use anthropogenic definitions of changes in composition and configuration (e.g., forest/non-forest, native grassland/crop fields). While these delineations often have important management and conservation implications, they may not be reflect strict habitat/non-habitat designations for the species of interest.

In Chapter 4 test four landscape change hypotheses for how pollination could be affected by disturbance. The first hypothesis is the *local* or *random-sample hypothesis* (Haila 1983). Under this scenario small patches are simply random samples of larger patches and only factors at the local scale or the level of individual plants should be important in determining pollination success. The second hypothesis is the *landscape composition hypothesis* (Fahrig 2003) where the amount of habitat in the landscape is important to pollination at scales larger than the individual plants. The *landscape fragmentation hypothesis* (Villard et al. 1999) anticipates that after controlling for effects of habitat loss, pollination failure should increase in a linear fashion with increasing fragmentation. Finally, the *fragmentation threshold hypothesis* (Andren 1994, Betts et al. 2006) is that landscape configuration is only important below some critical habitat amount. Under this hypothesis, we predict that reduced pollination should only occur in highly fragmented landscapes with low amounts of habitat cover.

I used a large-scale mensurative experiment (Hurlbert 1984) to disentangle the effects of local site characteristics, landscape composition, and landscape configuration on pollination of *Heliconia tortuosa*. I investigated the importance of scale at four different extents in this pollination system and in addition to testing typical anthropogenic composition measures (i.e., amount of mature tropical forest), I used an organism-based habitat model to quantify the amount of flowering *H. tortuosa* habitat available. I also quantify resource availability within the surrounding matrix. To my knowledge this is the

first attempt to disentangle the effects of composition and configuration in a tropical pollination system.

In the final section (Chapter 5) I discuss the findings of the three chapters outlined above. I list some limitations of this work, and suggest areas of promising new research.

THE EFFECTS OF LANDSCAPE FRAGMENTATION ON POLLINATION DYNAMICS: ABSENCE OF EVIDENCE NOT EVIDENCE OF ABSENCE

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2 THE EFFECTS OF LANDSCAPE FRAGMENTATION ON POLLINATION DYNAMICS: ABSENCE OF EVIDENCE NOT EVIDENCE OF ABSENCE

2.1 ABSTRACT

Animal-mediated pollination is essential for both ecosystem services and conservation of global biodiversity, but a growing body of work reveals that it is negatively affected by anthropogenic disturbance. Landscape-scale disturbance results in two often inter-related processes: (1) habitat loss, (2) disruptions of habitat configuration (i.e. fragmentation). Understanding the relative effects of such processes is critical in designing effective management strategies to limit pollination and pollinator decline. We reviewed existing published work from 1989 to 2009 and found that only six of 303 studies considering the influence of landscape context on pollination separated the effects of habitat loss from fragmentation. We provide a synthesis of the current landscape, behavioral, and pollination ecology literature in order to present preliminary multiple working hypotheses explaining how these two landscape processes might independently influence pollination dynamics. Landscape disturbance primarily influences three components of pollination interactions: pollinator density, movement, and plant demography. We argue that effects of habitat loss on each of these components are likely to differ substantially from the effects of fragmentation, which is likely to be more complex and may influence each pollination component in contrasting ways. The interdependency between plants and animals inherent to pollination systems also has the possibility to drive cumulative effects of fragmentation, initiating negative feedback loops between animals and the plants they pollinate. Alternatively, due to their asymmetrical structure, pollination networks may be relatively robust to fragmentation. Despite the potential importance of independent effects of habitat fragmentation, its effects on pollination remain largely untested. We postulate that variation across studies in the effects of 'fragmentation' owes much to artifacts of the sampling regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss, and (2) mismatches in spatial scale between landscapes studied and the ecological processes of interest. The field of landscape pollination ecology could be greatly advanced through the consideration and quantification of the

matrix, landscape functional connectivity, and pollinator movement behavior in response to these elements. Studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines, implementing effective conservation measures, and optimizing ecosystem services in complex landscapes.

2.2 Introduction

Most plant species depend on animal-mediated pollen flow (Ghazoul 2005) in order to enhance the directedness of pollen transfer among stationary flowers (Levin and Kerster 1969). Effective animal pollination is, therefore, extremely important for both ecosystem services [e.g., food production, medicine, carbon sequestration, flood control (Millennium Ecosystem Assessment 2005, Olschewski et al. 2006, Klein et al. 2007, Winfree et al. 2008, Potts et al. 2010)], and for conservation of global biodiversity, independent of human uses (Spira 2001, Bodin et al. 2006). Despite the lack of direct causal links, research showing large-scale parallel declines of plants and pollinators underscores the concern that pollination as a critical ecosystem function is at risk (Biesmeijer et al. 2006). Decreases in pollination and subsequent reduced plant fecundity are considered an early step in the demographic collapse of plant populations (Nason and Hamrick 1997, Aizen et al. 2002).

One prominent hypothesis is that such pollination declines are at least partly a function of processes occurring at larger, landscape scales (Kearns et al. 1998, Ghazoul 2005, Kremen et al. 2007). This hypothesis has recently stimulated the synthesis of two previously discrete fields in ecology: landscape ecology (Turner 1989) and pollination ecology (Müller 1883). Over the past decade, there has been an explosion of research that tests for the effects of landscape attributes on pollination dynamics (Steffan-Dewenter and Westphal 2008). Two recent meta-analyses revealed strong support for larger-scale drivers of pollination dynamics across multiple ecological systems and plant life-history traits (Aguilar et al. 2006, Eckert et al. 2010). However, the mechanisms behind such effects are unclear; little is known about which landscape attributes (e.g., habitat amount,

connectivity, patch size) or what components of the pollination system (e.g., pollinator density or movement, plant demography) drive frequently observed pollination failure. We argue that understanding such mechanisms is essential for testing ecological theory and for optimizing landscape design to deliver pollination services.

2.3 Landscape composition versus configuration

Landscape structure is defined by two major elements: composition and configuration (Turner 1989). Landscape composition is the type and amount of habitat or cover types within a landscape; therefore 'habitat loss' alters landscape composition. Landscape configuration reflects the spatial pattern or 'fragmentation' of landscape elements. Fragmentation *per se* refers to the spatial configuration of remaining habitat, independent of the amount of habitat within the landscape (Fahrig 2003). For instance, the degree to which patches within a landscape are connected by woodland corridors (Haddad 2008), or the size of patches themselves (Bender et al. 1998) are both aspects of landscape configuration (Fig. 2.1). Together, habitat loss and fragmentation are considered the primary threats to biodiversity worldwide (Pimm and Raven 2000). The importance of distinguishing between these two aspects of landscape structure is fundamental to metapopulation dynamics theory (Hanski and Ovaskainen 2000), reserve design and conservation of biodiversity in managed landscapes (Lindenmayer and Fischer 2007). Some theoretical models have revealed strong influences of configuration (i.e. patch size and connectivity) on rates of local extinction and therefore population viability (With et al. 1997, Hanski 1998). Therefore, management efforts at maintaining biodiversity have often focused on minimizing the effects of fragmentation (Saunders et al. 1991). Nevertheless, empirical support for influences of configuration on species distributions or demography is rare (Betts et al. 2006). This is in striking contrast to the nearly unequivocal support for the negative influences of landscape composition, particularly habitat loss, on biodiversity (Fahrig 2003).

However, it appears that the lack of evidence for negative consequences of fragmentation is less due to evidence of absence than to the absence of evidence; there is a dearth of well- designed studies testing for the influence of fragmentation. In a landmark paper,

Fahrig (2003) highlighted a fundamental problem in previous landscape ecological research testing for 'fragmentation effects'; in nature, landscape configuration and composition are usually confounded. That is, landscapes with large amounts of habitat are unfragmented while landscapes with low amounts of habitat also have small, unconnected patches. Only studies that separate these confounding effects statistically (McGarigal and McComb 1995, Trzcinski et al. 1999) or through experimental design (Tewksbury et al. 2002, Betts et al. 2006) can draw inferences about the independent effects of fragmentation. As of 2003 only three studies had successfully accomplished this task, and the problem is still relatively common in the landscape ecology literature (Lindenmayer and Fischer 2007). This is clearly problematic in terms of testing conflicting ecological theory regarding the relative importance of fragmentation and habitat loss. Indeed, debate over the relative importance of these landscape components has maintained a divide between the fields of landscape ecology and metapopulation biology (Hanski et al. 2006), the former minimizing the importance of landscape pattern (Fahrig 2001, Fahrig 2002, Prugh et al. 2008), the latter holding pattern to be a fundamental predictor of population dynamics (Hanski 1998). This is also an important quandary for conservation biologists who need to know which aspects of landscape structure to emphasize in reserve design and management (Collinge 1996). Why, if fragmentation and habitat loss are usually confounded in nature, is it of management interest to determine the independent effects of these variables? Though land use is often opportunistic and haphazard, across multiple biomes, policy tools exist or are being developed to enable detailed land-use planning toward conservation biology objectives (Moilanen et al. 2005, Kremen et al. 2008, Thomson et al. 2009, Smith et al. 2010); such planning provides the opportunity to generate landscape configurations that do not typically occur as part of the normal trajectory of human disturbance, but that are potentially beneficial to the conservation of biodiversity and/or ecosystem services.

Our first objective is to determine the degree to which the fragmentation hypothesis has been tested in the pollination literature. Here, we synthesize the existing work concerning the relative effects of habitat fragmentation (landscape configuration) and habitat loss

(landscape composition) on pollination. We also provide a synthesis of the current landscape, behavioral, and pollination ecology literature, to present preliminary multiple working hypotheses for explaining how these two landscape processes might influence pollination dynamics. By highlighting important knowledge gaps and pointing out promising new avenues of research we hope to assist the continued development of landscape pollination ecology.

2.4 Publication history of the effects of fragmentation on pollination

A substantial body of published work has focused on the effects of "habitat fragmentation" on plant reproduction, particularly pollination. To examine the current knowledge we conducted a search of the *ISI Web of Science* database. We searched for articles containing "frag*" and "poll*" in the topic field (Topic=[frag* AND poll*], Timespan=1970-2009, Databases=SCI-EXPANDED, SSCI.) and "Ecology" as a subject area option. This resulted in a list of 761 articles. While this is not an exhaustive list, we consider it to represent an unbiased sample of the existing literature. From these, we selected all of the articles examining the effects of landscape variables [both composition (e.g., habitat amount, habitat quality, matrix quality) and configuration (e.g., patch size, isolation, edge)] on plant pollination, fecundity or genetics. We also included articles examining the effects of landscape disturbance on pollinator demography or behavior. We conducted a detailed examination of the resulting 303 articles (see online supporting information Appendix S1) dealing with the effects of landscape disturbance on pollination systems. We considered a study to have examined independent effects of habitat loss and habitat fragmentation if the authors (1) controlled for habitat amount statistically, or (2) applied mensurative or manipulative experiments (sensu Hurlbert 1984). Statistical control constitutes including both habitat loss and fragmentation as predictor variables within the same multiple-regression model. Manipulative and mensurative experiments successfully disentangle habitat loss from fragmentation when these variables are independently varied using an *a priori* experimental design.

Since the publication of the first papers investigating landscape disturbance on pollination dynamics in the early 1990s the field of landscape pollination ecology has

grown rapidly (Fig. 2.2) and this growth is expected to increase (Millennium Ecosystem Assessment 2005, Natural Environment Research Council 2010). Of the 303 papers examining the effects of landscape disturbance on plant pollination services, 182 discussed their results as being the effects of habitat fragmentation. Fifty-eight included habitat fragmentation in their title. Studies often examined multiple combinations of landscape metrics and response variables (results are summarized in Table 2.1). While many of these articles measured configuration metrics (e.g., patch size, isolation, edge), only five empirical studies and one simulation study examined the independent effects of habitat configuration (Table 2.2). All others did not distinguish changes in landscape configuration from those of composition.

Unfortunately, these results provide strong evidence that though there has been great progress in testing for the influence of landscape-level changes on pollination success (e.g., Aguilar et al. 2006), the landscape pollination ecology literature has not yet effectively distinguished between the effects of landscape configuration and composition (Fig. 2.2). This is despite the fact that titles of articles imply that aspects of configuration have been tested (e.g., "Effects of fragmentation on pollination…"). Indeed, reviews and meta-analyses of the effects of landscape structure on pollination have generally implied that fragmentation has large negative effects on plant pollination (e.g., Ashworth et al. 2004, Aguilar et al. 2006). This confusion over the term 'fragmentation' prevalent in pollination ecology supports Fahrig's (2003) and Lindenmayer & Fischer's (2007) reviews of research on habitat fragmentation and biodiversity. Interestingly, these two key studies in landscape ecology (cited 676 and 30 times, respectively) appear to have had little effect in terms of stimulating research that separates landscape-scale drivers of pollination (Fig. 2.2). This does not detract from the importance of existing studies; the repeated finding that 'landscape structure' has strong influences on pollination (Aguilar et al. 2006) and pollinators (Winfree et al. 2009) is of critical importance. However, the question of which components of landscape structure are driving declines in pollination remains largely unanswered.

2.5 The importance of landscape disturbance in pollination systems

Pollination networks have been argued to be relatively robust and resilient to environmental perturbation (Bascompte et al. 2006); if a plant species depends strongly on an animal species, the animal depends weakly on the plant and overall, the number of strong dependencies is low. This observed asymmetry of pollination networks at the community level (Memmott et al. 2004, Bascompte et al. 2006) is thought to 'buffer' against landscape changes to some degree. However, declines in pollination success as a function of landscape disturbance (e.g., Kremen et al. 2002, Kremen et al. 2004, Aguilar et al. 2006) along with correlated negative responses by multiple species of native bees to increasing amounts of intensive agriculture (Winfree and Kremen 2009), suggest that aspects of highly altered landscapes are impacting pollination despite mutualistic network structures that promote robustness. Meta-analyses suggest that these landscape-mediated pollination declines are driven primarily through 'pollen limitation' (i.e., insufficient pollen delivery in disturbed areas; Aguilar et al. 2006) and/or reduced 'outcrossing rates' (i.e., lowered rates of pollen delivery from unrelated individuals; Eckert et al. 2010). However, the specific mechanisms behind reduced pollen quantity and/or quality are not well known (Eckert et al. 2010).

Animal-mediated pollination is a complex process by which plants capitalize on the mobility of their associated pollinators to reproduce sexually. Successful pollination depends on many interacting factors (e.g., number of flowers, distance between plants, number of pollinators, pollinator movement, pollinator diet breadth, phenology, pollen quantity *versus* quality, etc.; (Ghazoul 2005, Kremen et al. 2007). Landscape disturbance may influence pollination *via* altering three primary mechanisms: (1) plant density, (2) pollinator density, and (3) pollinator behavior (particularly movement). To facilitate uncovering the mechanisms behind pollination declines in disturbed landscapes, we briefly review the importance of these three primary mechanisms to pollination success (for more general discussion see: Ghazoul 2005, Kremen et al. 2007) and examine the potential for habitat loss and fragmentation to influence each component directly (Fig. 2.3).

2.5.1 Plant density

A change in the abundance, distribution or health of plants has the potential to influence pollination. Pollination success is related to both the number of conspecific flowers nearby (Feinsinger et al. 1986, Ellstrand and Elam 1993, Menges 1995, Kunin 1997, Waites and Agren 2004) and the distance between flowers within a patch (Bosch and Waser 1999, 2001). Plant health is important since it influences the size, number and quality of flowers which, in turn, is key for enhancing a plant's attractiveness to pollinators (Caruso et al. 2005). Changes in the surrounding plant community also affect interspecific competition for pollination (Levin and Anderson 1970, Caruso 1999, Chittka and Schurkens 2001). Plant density should be considered at multiple scales since it encompasses density of plants within patches, density of patches containing plants, and density of plant populations, all of which could influence plant and pollinator demography and pollinator behavior.

2.5.2 Pollinator density

The availability of pollinators in a landscape has a substantial impact on pollination systems. Both the abundance (Lennartsson 2002) and diversity of the pollinator community (Donaldson et al. 2002, Klein et al. 2003, Vázquez et al. 2005) have been found to predict pollination success. Landscape changes that increase or decrease the availability of pollinators could subsequently influence the effectiveness of the pollination systems involved.

2.5.3 Pollinator behavior

The availability of pollinators in a landscape or region does not ensure pollination. The effectiveness of available pollinators at pollen transfer depends on pollinator behavior. Changes in pollinator daily movements, including foraging extent (area covered in search of resources) and foraging pattern influence how pollen is distributed across the landscape (Kremen et al. 2007). Pollen can only be distributed along the movement paths of its pollen vectors, so areas left unvisited will clearly remain unpollinated. Conversely,

areas that are frequented more often or situated in high-traffic regions may receive higher rates of pollination (Tewksbury et al. 2002) and visit frequency appears to be a good predictor of pollination success (Jennersten 1988, Vázquez et al. 2005).

Pollinator foraging strategy is also a critical behavior since floral-specialist pollinators typically deliver higher quality 'pure' conspecific pollen loads (Levin and Anderson 1970, Ashman et al. 2004). Floral-generalist pollinators typically transport mixed pollen from several species and deliver larger amounts of incompatible pollen. This has been shown to block stamens and limit seed set (Brown and Mitchell 2001). Pollen loads can be further decreased when pollinators visit many different flower species within a foraging bout; conspecific pollen may be scraped from pollinators by the floral architecture of heterospecifics (Levin and Anderson 1970, Murcia and Feinsinger 1996). The presence of co-flowering plant species may also reduce pollination success by resulting in competition among different flower species for limited pollinator visits, thereby decreasing the delivery of species-specific pollen (Levin and Anderson 1970, Chittka and Schurkens 2001, Bell et al. 2005). This is particularly relevant as pollinator diet breadth is often context dependent; pollinators have been shown to switch from floral specialist to generalist strategies (or *vice versa*) depending on resource availability (Smithson and MacNair 1997, Chittka and Schurkens 2001, Fontaine et al. 2008). Such diet shifts can result in changes in visitation rates to competing plant species, individual inflorescences or individual flowers, all of which can significantly impact pollination success and have genetic consequences to plant populations (Ghazoul 2005).

2.6 Effects of habitat loss

The hypothesized negative effect of habitat loss on the first two mechanisms outlined above – plant and pollinator density – is relatively straightforward under most circumstances. Reducing the amount of habitat in the landscape (e.g., through land clearing) decreases conspecific plant density at the landscape scale. The negative effects of habitat loss on plant abundance, species richness and population size have been well documented (Laurance et al. 1999, Bascompte and Rodriguez 2001, Duffy 2003, Vellend

2003, Lindborg and Eriksson 2004, Helm et al. 2006, Harpole and Tilman 2007). Fewer plants results in reduced pollen availability in the system and more limited options for outcrossing. A reduction in effective population size lowers the number of pollen donors or receivers as well as the quantity of resources available to pollinators.

Similarly, habitat loss has been shown to have strong negative effects on pollinator abundance (Taki et al. 2007, Sjödin et al. 2008, Steffan-Dewenter and Schiele 2008, Winfree et al. 2009). Therefore, in most instances, habitat loss will reduce numbers of both plants and pollinators (see A and B in Fig. 2.3). This results in lower pollen availability and fewer vectors to move pollen through the landscape. Both of these mechanisms will likely reduce pollination success, particularly if the simultaneous reduction of many species overwhelms the buffering capacity of the pollinator network structure (Winfree and Kremen 2009).

In practice, because 'habitat loss' often occurs simultaneously with 'fragmentation', under some conditions its effects may be more complex than described above. Below, as a guide to future research, we provide some preliminary hypotheses for how the independent effects of fragmentation might influence pollination.

2.7 Effects of fragmentation

Given the absence of published work specifically devoted to the influence of habitat fragmentation *per se* on pollinators and pollination, we found it necessary to turn to broader research on the effects of landscape configuration on plants, animals, and animal behavior. Though this work is not specific to pollination, we expect that the processes driving fragmentation effects on plants and animals generally are likely to be pertinent to pollination systems.

2.7.1 Plant and pollinator densities

The effects of habitat fragmentation on plant and animal distributions are hypothesized to occur primarily as a result of alteration to three aspects of landscape configuration: patch

size, edge, and landscape connectivity (Bender et al. 1998, Bolger et al. 2000, Tewksbury et al. 2002). The effects of patch size are expected to influence demographic (Lande 1993) and genetic stochasticity (Whitlock 2004), local extinction (Hanski and Ovaskainen 2000), establishment (Bowman et al. 2002), habitat selection (Fletcher and Hutto 2008), animal predation of pollinators (Batary and Baldi 2004), resource quality (Burke and Nol 1998), and interspecific competition (Macarthur et al. 1972). Edge effects in plant and animal communities are common (Chen et al. 1992, Murcia 1995), but may be positive (Chen et al. 1992) or negative (Bruna 2002) and affect distributions, abundance (Bolger et al. 2000), growth (McDonald and Urban 2004), and reproduction (Burgess et al. 2006). Edge effects have been found to occur as a function of local micro-climatic influences (Murcia 1995) and elevated animal predation (Cantrell et al. 2001). A third component of landscape configuration, connectivity, has been found to affect rates of animal movement (see Section VI.2*a*) and therefore rates of dispersal and patch colonization (Haddad 2000).

Research on metapopulations has revealed the potential importance of landscape configuration to plant and animal population dynamics (Hanski and Ovaskainen 2000). Metapopulation ecology involves the study of discreet sub-populations occupying habitat patches within an unsuitable matrix (Levins 1969). Under equilibrium conditions, metapopulations are maintained *via* interaction among the sub-populations through individual dispersal. This approach to population dynamics emphasizes the importance of characteristics of populations that affect extinction (e.g., patch size) and dispersal rates (e.g., distance among patches) (Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2004). Metapopulation theory is particularly relevant to pollination dynamics in disturbed areas where interactions between plants distributed among patches is maintained primarily through pollinator movement. In addition, metapopulation models have been used to demonstrate the effects of patch size and connectivity on insect populations, many of which are pollinators (Wahlberg et al. 2002a, Wahlberg et al. 2002b, Hanski et al. 2006). Unfortunately, one legacy of early metapopulation approaches and the Theory of Island Biogeography (MacArthur and Wilson 1967) has been the adoption of a

dichotomous ‘patch’ (i.e. habitat) and ‘matrix’ (i.e. non-habitat) view of terrestrial landscapes that are usually far more complex (Fahrig et al. 2010); although some pollinators may be organized as metapopulations, distributions and movements may not correspond well to structurally defined patch/matrix delineations (Fischer and Lindenmayer 2006) and move readily across – and even use resources within – what may be expected as ‘non-habitat’ by the researcher (see Section VII).

Independent effects of habitat fragmentation on population density or distributions have been demonstrated empirically for several taxa including plants (Damschen et al. 2008, Brudvig et al. 2009), insects (Collinge and Forman 1998, With et al. 2002, Krawchuk and Taylor 2003), birds (Betts et al. 2006, Betts et al. 2007) and mammals (Collins and Barrett 1997). This suggests that independent effects of fragmentation on plant and pollinator densities may occur in many systems and taxa. Unfortunately, due to the paucity of studies on this topic, the generality and strength of these findings is debated (Prugh et al. 2008) and still not well understood.

2.7.2 Pollinator behavior

We anticipate that some of the most intriguing possibilities for independent fragmentation effects on pollination may stem from a third potential mechanism, ‘pollinator behavior’ (see E in Fig. 2.3). Such responses to fragmentation are likely mediated *via* changes in both pollinator movement and diet selection.

Movement effects. - Optimal foraging theory suggests that animals should forage in such a way as to maximize their energy intake per unit time (MacArthur and Pianka 1966). While the majority of existing work on animal movement has been conducted on vertebrate species for logistical reasons, we expect invertebrates to show similar behavioral responses at relevant scales. Movements between patches presumably have a cost; time is spent traveling which could otherwise be spent procuring resources (Hinsley 2000). Visiting small patches will be less profitable, particularly if inter-patch distance increases (Tentelier et al. 2006; Fig. 2.3C). These gap-crossing movements may also be risky and increase exposure to predation (Lima and Zollner 1996). For a variety of animals, including birds (Bélisle and Desrochers 2002) and mammals (Bakker and Van

Vuren 2004), gap crossing appears to be the primary risky behavior documented in fragmented landscapes and simulations have shown mortality occurring during movements between patches to be a major factor in population survival (Bender and Fahrig 2005). Animals may choose to cross small gaps, but with limited regularity or may choose longer indirect routes to circumnavigate (e.g., warblers; Desrochers and Hannon 1997, and hummingbirds; Hadley and Betts 2009). Gaps larger than a certain size may constitute obstacles due to animal physiological limitations (Moore et al. 2008) or the fact that distant resource patches are outside the organism's perceptual range (Lima and Zollner 1996, Conradt et al. 2001, Diekotter et al. 2007). Therefore, pollinators are likely influenced by both patch size and distance between patches when undertaking movement decisions. Visiting small patches will be less profitable, particularly as inter-patch distance increases (Tentelier et al. 2006; Fig. 2.4 [B,C]). Animal decisions regarding resource exploitation in fragmented landscapes are thus likely to be dependent on trade-offs between resource availability and risk (Turcotte and Desrochers 2003).

Though landscape-scale experimental studies are rare (Beier and Noss 1998), the few existing studies have shown that corridors increase movement rates for multiple animal taxa (Haddad et al. 2003). Preliminary evidence suggests that corridors or at least increased 'functional connectivity' - the degree to which the landscape facilitates or impedes movements between resource patches (Taylor et al. 1993) - can facilitate the movements of pollinators (Haddad 1999, Haddad 2000) and increase subsequent pollination success (Townsend and Levey 2005; Fig. 2.4F).

Habitat edges often have profound impacts on animal movements and if pollinators show similar responses, the pattern of edges in a landscape could have strong implications for pollen movement. Evidence exists for animals both avoiding (Dolby and Grubb 1999) and associating with edges (Desrochers and Fortin 2000, Hadley and Desrochers 2008) during their daily movements. Edges may differ from interior regions in terms of predation risk (Ibarzabal and Desrochers 2004) and their profitability (Thompson and Willson 1978) leading to behavioral decisions to avoid these areas. Edges can also direct

or channel animal movements simply by acting as a movement conduit (Desrochers and Fortin 2000). In this manner, edges can direct the movements of an animal even deep within the patch (Desrochers and Fortin 2000).

By altering pollinator movements, fragmentation could also facilitate pollination in certain instances. For example, Brosi, Armsworth & Daily (2008) and Keitt (2009) found that if foraging movements of pollinators are limited in Euclidian distance, landscape designs that intersperse pollinator habitat with floral resources (i.e. a highly fragmented landscape) could be preferable. Indeed, Winfree *et al.* (2008) recommended this approach to maximize crop visitation by native pollinators; they proposed forested hedgerows embedded in agricultural landscapes to facilitate crop access for solitary tree-cavity-nesting bees. Similarly, Holzschuh, Steffan-Dewenter & Tscharntke (2008) showed that interspersion of organic crops increased native bee diversity in landscapes dominated by conventional wheat fields. However, it is important to note that these designs represent a particular circumstance where the objective is maximization of crop pollination. While such landscape patterns may facilitate pollination of agricultural crops, they might not have similarly positive consequences for the native plants depending on these same pollinators. Interspersion of high-reward flowering crops could actually disrupt networks and reduce the availability of pollinators for native plants (Aizen et al. 2008). Further, such recommendations need to be placed in the context of pollinator population dynamics. If large patches have lower probabilities of pollinator extinction, as would be expected under metapopulation theory, a mix of small interspersed, and large contiguous patches might be optimal for pollination services (Brosi et al. 2008).

Under some circumstances, fragmentation could also facilitate outbreeding (Heinrich and Raven 1972). In fragmented systems with patchily distributed plants, pollen delivery from distant individuals should be more frequent when floral specialist pollinators are forced to cover larger areas to procure sufficient resources (Fig. 2.5). Although quantity of pollen should decrease for the reasons highlighted above (see Section IV.1), quality of pollen delivered could potentially improve due to higher amounts of outcross pollen from more distant conspecific plants (Dick 2008). Further, in some instances, the frequency of

flower visitation appears to increase in smaller patches (Goulson 2000, Diekotter et al. 2007). Visiting a smaller proportion of inflorescences as patch size increases is expected to be an optimal strategy (Goulson 2000). Provided inter-patch movement is unimpeded, such behavior could facilitate *per capita* plant reproductive success in small patches. Such scenarios should only be possible in systems with highly mobile, habitat-generalist pollinators whose movements are unencumbered by fragmentation.

Diet selection. - Pollinator diet selection is important to pollination success since it affects the number of visits to flowers (Bell et al. 2005) as well as the quality of pollen delivered (Aizen and Harder 2007). Pollinator foraging preferences are often plastic and vary depending on the characteristics of the plant community in which they forage (Fontaine et al. 2008). Introduction of invasive species (Chittka and Schurkens 2001, Aizen et al. 2008) and changes in heterospecific flower densities (Jakobsson et al. 2009) have both been shown to decrease pollination success. Since plant densities, relative flower abundance (e.g., native/invasive) and flower quality (e.g., number of inflorescences, display size) can all be affected by landscape configuration (particularily edge effects; Murcia 1995, see 'Plant Density' above) it follows that pollinator foraging behaviors may also be fragmentation sensitive.

Visitation rates to individual flowers have been shown to differ depending on patch size (Cresswell and Osborne 2004) and resource density (Kunin 1997). Flower quality is also a factor in visitation (Grindeland et al. 2005) that can vary with proximity to edge (Jules 1998). These increases in flower abundance and quality have been hypothesized to drive higher pollinator abundances next to edges (Stouffer and Bierregaard 1995). Therefore, we expect foraging patterns in fragmented areas with modified flowering communities to differ from behavior in unfragmented landscapes.

Fragmentation *per se*, therefore, has the potential to influence pollination dynamics by directly affecting pollinator or plant densities and altering pollinator behavior (movement, diet). Because plant and animal taxa might respond to landscape

configuration in contrasting ways, the effects of landscape fragmentation will likely be complex.

2.8 Defining habitat and matrix

2.8.1 Habitat

Properly defining landscape elements is a critical component of landscape ecology (Wiens 1995). In order to examine the effects of landscape disturbance on pollination it is important to quantify changes that have occurred and the characteristics of the habitats that remain. Definitions of 'habitat' are inherently species specific; attributes such as habitat amount, patch size and connectivity often differ greatly among plant or pollinator species even within the same landscape (Addicott et al. 1987, Betts et al. 2007, Holzschuh et al. 2010). To address this issue, the 'species-centered approach' (Fig. 2.6) uses species distribution models to quantify landscape elements from the perspective of individual species (Betts et al. 2006). This approach has now been used to explain species occupancy and demography as a function of habitat loss and fragmentation (Betts *et al*., 2007; Zitske, Betts & Diamond, 2011). However, applying this method is more complicated in landscape pollination ecology because plants and their associated pollinators may perceive the landscape in different ways (Cane 2001); though it seems intuitive that habitat for a plant is also habitat for its pollinators, this is not necessarily the case. Habitat from the plant's perspective comprises the suite of different abiotic and biotic characteristics that permit their growth and reproduction at a single site (Bazzaz 1991). Habitat from the pollinator's perspective is often more complex because each life-history requirement may necessitate different compositional and structural features occurring across multiple sites (Lima and Zollner 1996). Foraging, breeding and movement habitats are spatially discrete for many species (Westrich 1996). For instance many native bee pollinators nest in forest, but forage in the surrounding cropland (Ricketts 2004, Sande et al. 2009). Alternatively, some pollinators appear to have high fidelity to nesting and movement habitats that co-occur with food plants (e.g, Stiles 1975). Regardless, it is critical that the definitions used to characterize landscapes are pertinent to the questions and organism considered (Cane 2001). A variety of powerful

tools are now available to model the distribution of plants and pollinators – even when only presence data are available (Phillips et al. 2006). Though it might seem obvious that landscapes should be quantified using an organism-based approach, we found many studies that test for the influence of landscape structure on species distributions and pollination based on landscape features that are primarily relevant to humans and/or easily measurable (e.g., amount of forest cover, distance between forest patches). Such variables do not necessarily correspond to the ecological processes themselves.

The spatial scale of research should also be justified in biological terms (e.g., Kremen et al. 2002, Holzschuh et al. 2010) rather than logistical constraints since choice of scale can have dramatic effects on results (Willis and Whittaker 2002). The spatial scale of research should be relevant to both daily foraging movements and often larger-scale population dynamics of pollinators (Brosi et al. 2008). Ignoring these considerations risks Type II error where it is concluded that 'fragmentation' of landscapes is irrelevant to pollination, when absence of detected effects is purely a result of incorrect initial definitions of landscape structure (Betts and Villard 2009). For example, though they did not consider the independent effects of fragmentation, Lonsdorf *et al.* (2009) contributed an important advance by quantifying guild-specific pollinator nesting resources, floral resources and foraging distances to estimate the relative abundance of pollinators, and therefore pollination services, across agricultural landscapes. Conversely, small-scale manipulations successfully examining independent fragmentation effects (Cresswell and Osborne 2004, Diekotter et al. 2007) may not reflect natural landscape disturbance levels of conservation interest or pollinator dispersal distances (Osborne et al. 1999).

2.8.2 Matrix

The vast majority of studies we reviewed considered habitat loss and fragmentation as a dichotomous process, reflecting habitat patches as islands in a sea of uniform, unsuitable space. Though this approach facilitates easy landscape measurement, as noted above it has become increasingly clear that this view is an over-simplification in most landscapes (Jules and Shahani 2003). The characteristics of the intervening 'matrix' of landscape

elements separating habitat patches have the potential to influence pollinator movement among patches (Fig. 2.4) and the quality of the intervening matrix can either mediate or exacerbate the influence of fragmentation (Bender and Fahrig 2005). For example, in many instances – particularly in forested or less intensively managed agricultural landscapes – distinctions between 'patch' and 'matrix' may be subtle (Fig. 2.6). A relatively favourable matrix may actually enhance the quality of remaining patches through increased resource availability (a process termed 'habitat supplementation'; Dunning et al. 1992) and may reduce movement resistance (Brotons et al. 2003). Matrix resistance is species specific and is a function of behavioral avoidance (Hadley and Betts 2009), physical crossing ability (Moore et al. 2008), and/or the organism's perceptual range (Lima and Zollner 1996). Presence of sufficient resources for foraging may also influence matrix permeability. In most systems, the matrix presents varying levels of resistance to animal movements, ranging from a complete barrier (Moore et al. 2008) to offering relatively little opposition or even facilitating movement (Fig. 2.6A). For instance, in a small-scale experiment, Diekotter *et al.* (2007) found that abundance of pollinators, flower visitation and seed set were higher in clover patches surrounded by bare ground than grass matrix.

Recently there has been a great deal of progress in measurement and quantification of landscape resistance to animal movement using 'graph theoretic' approaches. Graph theory is a body of mathematics designed to address problems of connectivity, flow and routing in networks (Adriaensen et al. 2003, Urban et al. 2009). Spatial graphs based on empirically derived pollinator movement resistances could be incorporated into statistical models predicting pollination success as a function of functional connectivity for pollinators (see Section VIII and Fig. 2.7).

2.9 Measuring connectivity in plant-pollinator systems

Corridors, defined here as structural connections between habitat patches, may often be the exception rather than the rule in fragmented landscapes, so it is important to understand how dispersal connections through the matrix affect pollination dynamics across the landscape (Minor et al. 2009). One commonly adopted technique in landscape

ecology for measuring connectivity (S_i) involves the use of the incidence function model (IFM) equation:

$$S_i = \sum \exp(-\alpha d_{ij}) A_j^b \quad (1)$$

where d_{ij} is the distance between a focal patch i and patches j, A_j is the area of patch j, with parameter α scaling the effect of distance on dispersal (1/α is the average pollinator movement distance), and b is a parameter scaling the effect of emigration to the area of surrounding patches (Hanski 1994). The parameter α has previously been estimated using passive observations of marked animals (Wahlberg et al. 2002a). The second parameter, b, can also be estimated using mark-recapture data – though performance of IFMs is not tremendously sensitive to this parameter (Prugh 2009). The IFM thus takes into account the exponential decay typical of dispersing propagules (in this case pollen) as well as hypothesized relationships between the likelihood of pollinator immigration and emigration in relation to the area of surrounding patches. Though a variety of connectivity metrics have been applied in the literature, IFMs are thought to be superior because they contain information about the entire patch network (i.e. the size and distance of neighbouring patches) in relation to species dispersal or movement abilities (Bender et al. 2003, Minor et al. 2009, Prugh 2009).

It is particularly important to consider functional connectivity from the pollinator's perspective as it is not necessarily dependent only on the configuration of plant habitat. Connectivity measured using the Euclidian distance between patches of plants or flowers may not accurately represent patch connectivity if relative resistance of the intervening landscape elements to pollinator movements varies (Fig. 2.7; see Section VII.2). A key challenge in adopting a species-centered approach in landscape pollination ecology will be the acquisition of landscape data at sufficient spatial resolution to be relevant to pollinator behavior (Lonsdorf et al. 2009).

Measuring functional connectivity is notoriously difficult as it necessitates determining the motivation underlying the individual movement (Bélisle 2005); for instance, lack of movement by a pollinator across an apparent habitat gap could reflect a physical

impediment, or simply a lack of motivation (e.g., resources are sufficiently available without necessitating gap crossing). Experimental manipulations to standardize motivation coupled with precise tracking methods are likely to offer the most meaningful assessment of functional connectivity in the field. Techniques relevant to pollinators include translocation, food-titration experiments, giving-up density experiments, and manipulation of nest location. Translocation (Hadley and Betts 2009) might be particularly useful for territorial pollinators with homing tendencies since the destination and motivation of individuals is controlled; individuals can be moved across specific landscapes differing in composition or configuration and their return path/success monitored. However, the strength of translocation experiments may simultaneously be their weakness; the behavior of pollinators on translocation does not necessarily correspond to the behavior of pollinators during daily movements. Studies comparing behavior on translocation with 'natural' movement behavior are urgently required. Food-titration experiments (Turcotte and Desrochers 2003) set up using floral arrays or feeder units in different landscape contexts could be used to assess gap-crossing abilities and perceptual range. Similarly, aspects of marginal value theorem such as 'giving-up density' (GUD) or 'giving-up time' (GUT) experiments can also reveal interesting results relating to foraging decisions under different landscape contexts. Such experiments could examine the number of flowers that remain unvisited in a patch when a forager moves to a new patch, or the amount of time spent at a patch before emigration. Pollination systems appear extremely conducive to these sorts of experiments (e.g., Collevatti et al. 1997, Goulson 2000, Diekotter et al. 2007). Manipulating nesting site location (e.g., placement of hives; see Taki et al. 2010) with respect to known landscape characteristics and food resources may also be useful in determining minimum requirements for persistence.

Because functional connectivity is a species-specific concept (Taylor *et al*., 1993) for many pollinators it may be more appropriate to measure distance between patches (*d*) in the incidence function model (equation 1) using cost distance modeling (Bunn et al. 2000) rather than Euclidian distance. This approach has usually relied on experts to

estimate the expected 'resistance' values of various types of intervening matrix on a species-specific basis (e.g., Driezen et al. 2007). A more rigorous approach could be to quantify landscape resistance (i.e. movement costs) *via* functional connectivity experiments as outlined above. Urban *et al*. (2009) argue that using detailed movement trajectories of translocated animals is the most promising method for parameterizing least cost paths – though data to accomplish this are rare. As an initial demonstration of such an approach, we quantified functional connectivity for a traplining hummingbird species using observed movement paths (see Fig. 2.7 for details).

2.10 Sensitivity of pollination to habitat fragmentation

Pollination might be relatively insensitive to fragmentation for several reasons. First, as a general rule, effects of habitat fragmentation on biodiversity are often thought to be relatively modest in comparison to habitat loss (Fahrig, 2003). In addition, pollination may be buffered against changes in landscape configuration due to the structure of plant-pollinator networks (Memmott et al. 2004). As noted above, the nested structure typical of plant-pollinator networks means that most specialized plant species are visited by generalist pollinators and *vice versa* (Bascompte et al. 2006). Specialist plants are visited by multiple pollinator species, each of which may display differential sensitivity to landscape characteristics. As landscapes become more fragmented for a pollinator with poor vagility, precluding efficient inter-patch movement for this species, another more vagile species could be expected to adopt the key pollination role. Further, because, by definition, floral-generalist pollinators are capable of using a wider range of floral resources, generalist pollinators are likely to perceive landscapes as having larger amounts of habitat and lower degrees of fragmentation (see Fig. 2.6A). Specialist plants occurring in isolated patches may therefore still have access to high abundances of generalist pollinators. For these reasons, at the community level at least, there may be robustness in pollination systems to both habitat loss and fragmentation.

However, though the structure of pollination networks has been examined across gradients in such stressors as invasive species (Aizen et al. 2008) and habitat loss

(Sabatino et al. 2010), to our knowledge, no such study has been completed for landscape fragmentation *per se*. Repeated findings of negative effects of landscape disturbance (habitat loss and fragmentation combined) on pollination success (e.g., Kremen et al. 2002, Kremen et al. 2004, Aguilar et al. 2006) suggest that it cannot necessarily be assumed that the nested nature of pollination networks offers effective buffering against all disturbances. Buffering in pollination networks is hypothesized to break down under conditions of extreme cases of habitat loss or fragmentation where densities of many interacting species simultaneously decrease below certain thresholds (see 'Landscape Thresholds' below; Fortuna and Bascompte 2006). Further, if entire functional groups of pollinators respond to fragmentation in similar ways, buffering capacity would be lost. Finally, fragmentation could potentially affect critical 'hub' species in networks (Olesen et al. 2007); through the loss of a single generalist species multiple links could be removed thwarting much of the network's capacity to buffer. Functionally efficient pollinators may also be those that are most extinction prone contributing to rapid loss of function; indeed, Larsen, Williams & Kremen (2005) demonstrated that habitat loss resulted in preferential loss of such efficient pollinators. For these reasons, we suggest that fragmentation should not be dismissed as a driver of widespread pollination declines until its relative contribution has been quantified.

Despite the fact that there are theoretical reasons for both positive and negative effects of fragmentation, we feel that the potential for negative responses deserves special attention. Unlike Fahrig (2003), who found that effects of habitat fragmentation on biodiversity were as likely to be positive as negative, four of the five existing empirical studies controlling for the effects of habitat amount showed negative effects of habitat fragmentation on pollination. The independent fragmentation effects in pollination systems may not be trivial (Table 2.2).

As an alternative to the hypothesis that pollination networks will be buffered due to their asymmetrical structure, we suggest some hypotheses for the potential sensitivity of pollination dynamics to fragmentation *per se*. These hypotheses are most likely to apply

and be detected in landscapes where distinctions between native habitat and non-habitat are clear (Kremen et al. 2002) and where plant and pollinator habitats are approximately congruent (e.g., forest systems; Aizen and Feinsinger 1994). First, pollination is multi-faceted (Hegland *et al*., 2009, but see Memmott *et al*., 2004), and requires efficient functioning of three major ecosystem components or processes (i.e. plant density, pollinator density, pollinator behavior) interacting at multiple spatial scales (e.g., plant, patch, landscape). Failure or decline in any of these components or processes is likely to result in reduced or failed pollination, at least at the level of individual plant species. Though changes in plant and pollinator density or pollinator behavior alone could be sufficient to reduce pollination, there is also potential for initiation of negative feedback loops (Fig. 2.3). For example, reduced plant fecundity in fragmented landscapes, as an initial result of inefficient pollinator movement (Levey et al. 2005), would eventually result in lower plant density unless inter-patch seed dispersal is biased toward fragmented patches. Low plant densities in fragmented patches should further reduce the benefits to pollinators of visiting these patches (Heinrich and Raven 1972). We hypothesize that the cumulative interacting effects among the different mechanisms outlined above could contribute to fragmentation sensitivity of pollination systems beyond those observed for individual plant or animal species.

Second, landscape configuration can change animal movement rates and patterns even when there is no measurable effect on density or abundance. For instance, despite higher densities of hermit hummingbirds (*Phaethornus* sp.) in fragmented landscapes (Stouffer and Bierregaard 1995), landscape fragmentation negatively affects movement (Hadley and Betts 2009). It is important to consider pollination in terms of a network with variable levels of flow (Dalsgaard et al. 2008). If pollinators avoid crossing non-habitat during their daily movements and alter their movement patterns accordingly (Hadley and Betts 2009) we would expect to see differences in the volume and pattern of pollen movement in relation to intact landscapes. If matrix inhibits movement, maintaining connectivity among patches may be crucial for inter-patch pollen flow (Fig. 2.4F). Plant

species requiring outcrossing events (i.e. those that are self-incompatible) may be sensitive to even slight reductions in inter-patch movements.

Finally, the requirement for repeated animal movements between flowers and/or patches to obtain sufficient resources for persistence (i.e. landscape supplementation) also makes pollination more vulnerable to the risks posed by fragmentation. Animal dispersal usually only requires a single movement event to a patch during an organism's lifetime to colonize isolated patches and maintain metapopulations (Hanski 1998); however, if there are insufficient resources within a single patch (Tiebout 1991), nectar collection requires repeated inter-patch movements by the same individuals. For example, in our tropical montaine forest study system, traplining hummingbirds depend on relatively rare, yet high-reward flowers (Stiles and Freeman 1993), so repeated daily inter-patch movements are necessary, which may result in more chronic risk (Hinsley 2000). Mortality risk during movements within the matrix can have a substantial impact on metapoplulation dynamics even when only a single crossing event is required (Fahrig 2002). Longer-distance foraging bouts under situations with sparse resources have been shown to reduce pollinator reproductive success (Goodell 2003).

2.11 A NOTE ON LANDSCAPE THRESHOLDS

Previous theoretical (Fahrig 1998) and empirical work (Andren 1994, Radford et al. 2005, Betts et al. 2007, Tscharntke et al. 2008) has demonstrated that the effects of fragmentation are often non-linear. That is, negative effects of fragmentation only occur in landscapes with low amounts of habitat. Though few studies have tested for landscape thresholds in pollination, a study on orchids, *Ptergodium catholicum*, indicated that habitats <385 ha, when separated by urban matrix, were too small to maintain populations of the orchid's sole bee pollinator, *Rediviva peringueyi* (Pauw 2007). Fragmentation thresholds tend to be relatively low in simulation models (~10% habitat; Fahrig 1998) and empirical studies (10-30%; Andren 1994). However, theoretical work has tended to focus on one-time negative consequences of natal dispersal in fragmented landscapes. Therefore, unless mortality in non-habitat matrix is extremely high (With et

al. 1997, Fahrig 2001), most models reveal relatively small effects of fragmentation even at low habitat amounts (Fahrig 1998).

Because of the possibility for independent effects of fragmentation noted above and the potential for among-taxa interactions, which may drive negative feedback loops, in some systems it might be expected that thresholds in pollination dynamics occur at higher levels of habitat than in the case of individual species' demography. Indeed, a recent simulation study which tested for the independent effects of habitat loss and fragmentation on pollination showed that, owing to such feedbacks, plant-pollinator networks can be disproportionately sensitive to landscape changes; extinction thresholds in pollination networks occurred at 50-60 % habitat loss (Keitt 2009). If limitations to foraging or dispersal due to fragmentation are incorporated, extinctions occurred at even higher habitat amounts (Keitt 2009). In simulation models, loss of key species within a community is thought to lead to sudden collapse (Kaiser-Bunbury et al. 2010) indicating that rates of decline may not be easily predictable. Despite these points, it is still possible that thresholds could be lower rather than higher, due to the buffering capacity provided by the nestedness of pollination networks (Fortuna and Bascompte 2006) or if pollinator species are not narrowly tied to the natural habitat type, but capitalize on resources in the matrix.

There are now a variety of statistical tools available to quantify and test statistically for thresholds (Muggeo 2003, Toms and Lesperance 2003) so such testing alternative hypotheses regarding the existence and sensitivity of thresholds in pollination systems seems a productive avenue for future research given appropriate empirical data; to our knowledge no threshold models have yet been applied in pollination studies. Finally, future simulation models should consider the cumulative effects posed by the regular gap-crossing behavior of species requiring multiple resource patches to satisfy their life-history requirements (sensu Dunning et al. 1992).

2.12 Implications for future research and conservation planning

Given the high degree of uncertainty about the effects of fragmentation on pollination systems beyond those attributable simply to habitat loss (Fig. 2.3), it will be particularly important to consider configuration in future landscape pollination ecology studies. The fact that, in nature, the processes of habitat loss and fragmentation often occur together and are correlated does not imply that there is no scientific or conservation need to disentangle them. Without understanding the drivers of pollination and pollinator declines it will be impossible to conceptualize optimal landscape designs for maintaining or enhancing pollination services (Brosi et al. 2008, Lonsdorf et al. 2009; e.g., Fig. 2.1). Though the existing body of literature has done much to elucidate the importance of landscape structure as a whole on pollination dynamics, failure effectively to separate the independent effects of composition and configuration has hampered the potential to identify causes of the revealed patterns. We expect that variation across studies in the effects of 'fragmentation' owes much to artifacts of the sampling regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss and (2) mismatches in spatial scale between landscapes studied and the ecological processes of interest. Here, we provide three recommendations to facilitate research in the field of landscape pollination ecology.

First, more emphasis should be placed on designing studies that disentangle the different aspects of pollination in disturbed landscapes. Landscape disturbance clearly has negative impacts on pollination in most systems (Aguilar et al. 2006). These effects may be partly due to changes in the plant community (Honnay et al. 2005) or to changes in the pollinator community and behavior (Steffan-Dewenter and Westphal 2008). Controlled, replicated experiments such as conducted by Tewksbury *et al.* (2002) and Townsend & Levey (2005) on movement corridors are ideal, but may become intractable if the objective is to consider the complexities of connectivity associated with different sorts of matrix. Since large-scale landscape manipulations are challenging and expensive, mensurative experiments designed explicitly to disentangle the role of various landscape elements may be the most effective (Betts et al. 2006). In cases where data have already

been collected or correlated variables are unavoidable, attempts should still be made to disentangle effects statistically (Smith et al. 2009).

Second, despite the multitude of ways that pollinator movement ability and movement decisions affect pollination services, we still know very little about even basic movement patterns of pollinators (Ghazoul 2005). Thus, the 'pollinator movement' hypothesis – that observed effects of landscape disturbance are due to restrictions in movement rather than plant or pollinator density – still remains largely untested. Testing this hypothesis will require the integration of pollination, landscape and behavioral ecology. Future work could be a combination of experimental and observational studies, designed to understand better the movement capacities and behavioral decisions of pollen vectors in relation to the spatial distribution of resources. Critical information will be required on animal dispersal distances, daily movement distances, gap-crossing capacities, movements in relation to edges, energy requirements and optimal foraging decisions. Recent technological improvements including reductions in the size of radio transmitters (Wikelski et al. 2006), harmonic radar (Osborne et al. 1999, Riley et al. 2005) and radio-frequency identification devices (Ohashi et al. 2010) provide the opportunity to observe movement behavior of pollinators across unprecedentedly large gradients in spatial and temporal grain and extent. Studies should be designed to examine landscape resistance and determine functional connectivity for pollinators and therefore associated plants (Bélisle 2005, Hadley and Betts 2009).

Finally, further progress in this field will require consistency in terminology and clear methodologies. We stress the recommendations of Fahrig (2003) and Lindenmayer & Fisher (2007) that the term 'fragmentation' should be reserved for the independent effects of landscape configuration while the term 'habitat loss' should reflect changes in landscape composition. If a study is not able to separate composition from configuration, using the terms 'landscape disturbance' or 'landscape-level effects' would avoid inaccurately assigning a result to either process and further propagation of the confusion that arises from using the same term to describe critically different processes. Studies

should clearly state and describe (1) the response variables of interest, (2) the spatial scale(s) of examination, (3) landscape-scale predictor variables and whether or not these represent landscape composition or configuration. Reporting the effect sizes of composition and configuration variables from multivariate statistical models (sensu Smith et al. 2009) is essential for interpretation of results, and will be essential for future meta-analysis on this topic. We hope that following these general guidelines will help direct crucial future work on the effects of habitat fragmentation on pollination.

2.13 Conclusions

(1) Landscape-scale disturbance results in two often inter-related processes: (1) habitat loss, (2) disruptions of habitat configuration (i.e. fragmentation). Understanding the relative effects of such processes is critical in designing effective management strategies to limit pollination and pollinator decline.

(2) We reviewed existing work and found only six of 303 studies considering the influence of landscape context on pollination separated the effects of habitat loss from fragmentation (Fig. 2.2). Therefore, almost no research exists on whether landscape composition (i.e. the relative abundance of land cover types, particularly the amount of habitat) or landscape fragmentation (e.g., corridors, patch size and shape), or both, are most critical to pollination dynamics (Table 2.2).

(3) Landscape disturbance primarily influences three components of pollination interactions: pollinator density, pollinator movement, and plant demography (Fig. 2.3). We argue that effects of habitat loss on each of these components are likely to differ substantially from the effects of fragmentation, which is likely to be more complex and may influence each pollination component in contrasting ways.

(4) Given the high degree of uncertainty about the extent to which fragmentation affects pollination systems, we argue that is it particularly important to consider configuration in future landscape pollination ecology studies. Without understanding the drivers of

pollination and pollinator declines it will be impossible to conceptualize optimal landscape designs for maintaining or enhancing pollination services (Fig. 2.1).

(5) We expect that variation across studies in the effects of 'fragmentation' owes much to artifacts of the sampling regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss and (2) mismatches in spatial scale between landscapes studied and the ecological processes of interest. We suggest that researchers adopt an organism-based view of the landscape and measure elements of interest accordingly.

(6) We provide three main recommendations for future studies. (1) Studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines, implementing effective conservation measures, and optimizing ecosystem services in complex landscapes. (2) We recommend a combination of experimental and observational studies, designed to understand better the movement capacities and behavioral decisions of pollen vectors. (3) Further progress in this field will require consistency in terminology and clearly defined methodologies.

ACKNOWLEDGMENTS

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TABLE 2.1. Summary of 303 articles examining the effects of landscape changes on pollination systems. Entries represent the number of times articles have attempted to investigate the given combination of variables. Each study may contain more than one metric and response variable. Reviews were excluded. The number of instances where configuration effects were successfully examined independent of composition is shown in bold.

	Response variables								
Landscape metrics	Pollination (70)	Pollen movement (13)	Seed set (67)	Genetic diversity (45)	Visitation rates (31)	Pollinator abundance/ diversity (44)	Pollinator movement (16)	Pollinator diet shift (5)	Pollination syndrome (3)
Habitat loss (33)	12	0	5	4	5	14	1	2	1
Patch size (102)	31	2	40	16	17 **(2)**	14 **(1)**	1	2	1
Isolation (90)	28	7	23 **(1)**	25	11 **(2)**	14 **(2)**	2	1	1
Corridors (3)	1	2 **(1)**	0	0	0	0	2	0	0
Edge (13)	3	0	3	0	1	7	2	0	0
Matrix quality (8)	0	0	1	2	2	2	2	0	0
Habitat degradation (19)	6	0	4	2	4	4	1	1	0
Disturbed *versus* undisturbed (30)	6	4	6	6	2	6	5	0	1

TABLE 2.2. Details of the five empirical studies examining the independent effects of configuration on pollination systems. -, negative effects of fragmentation; ns, no significant effect; na, not available. Terminology used in the actual studies was revised for consistency and to reflect the most commonly accepted term for each landscape metric.

Study	Configuration metric/response variable	Effect	Pollinator	Region	Landscape size (ha)	Separation method
Cresswell & Osborne (2004)	patch size/visitation rates	-	bees	temperate	3.38	manipulative experiment
	isolation/visitation rates	ns				
Townsend & Levey (2005)	corridors/pollen movement	-	bees/butterflies	temperate	40.72	manipulative experiment
Diekotter *et al.* (2007)	patch size/seed set	ns	bees/butterflies	temperate	0.02	manipulative experiment
	patch size/visitation rates	ns				
Steffan-Dewenter & Schiele (2008)	patch size/pollinator abundance	-	bees	temperate	na	statistical
Farwig *et al.* (2009)	isolation/seed set	-	flies/bees	temperate	78.54	mensurative experiment
	isolation/visitation rates	ns				

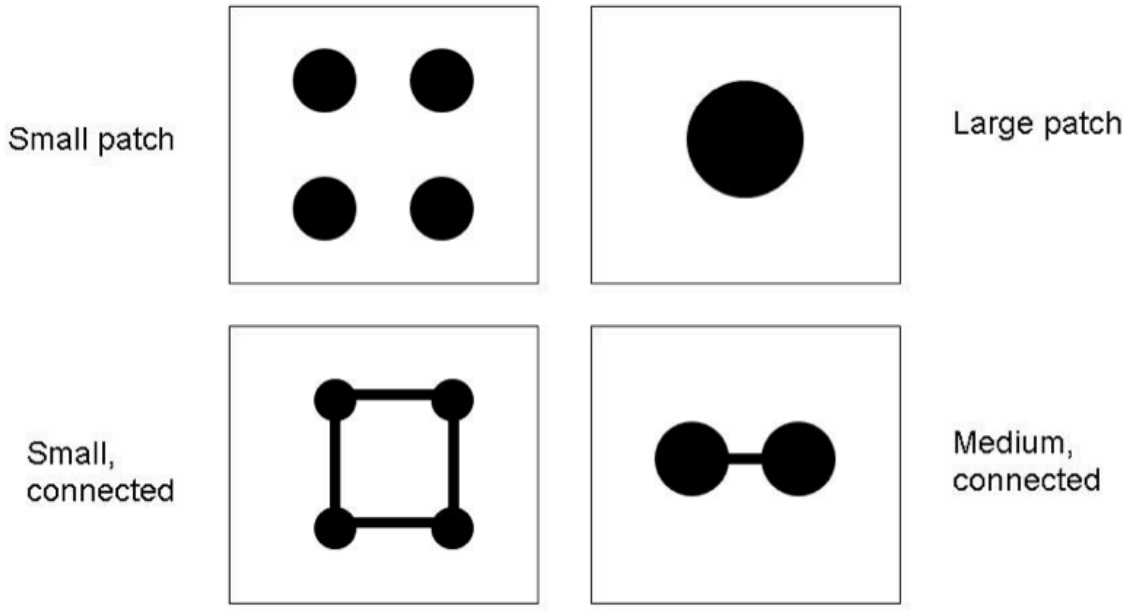

FIGURE 2.1. Examples of four possible landscape configurations with the same total amount of habitat, but with varying spatial configuration (patch size, connectivity). Depending on life history and ecological characteristics of plants and pollinators, each configuration could have dramatically different consequences for pollination dynamics.

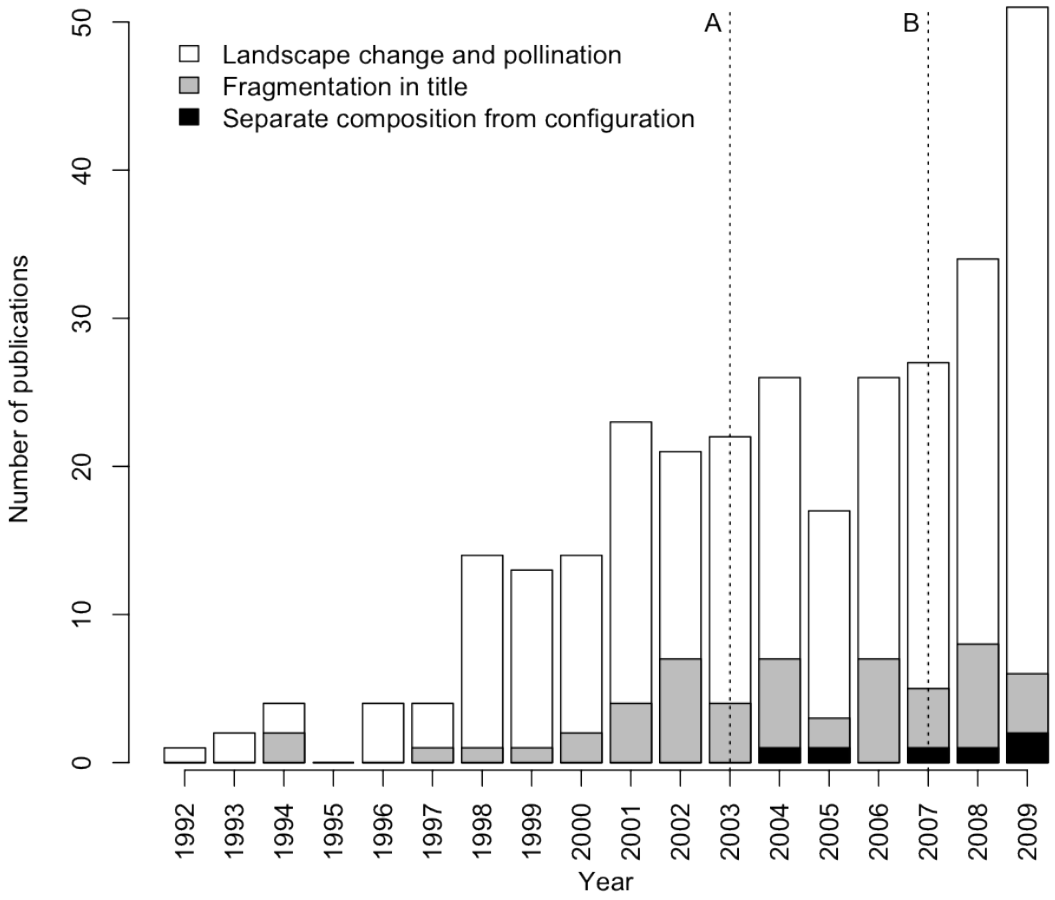

FIGURE 2.2. The number of articles published on the supposed 'effects of habitat fragmentation' in pollination systems divided into those failing to separate the effects of habitat loss from habitat fragmentation (white bars) and those studies properly separating the effects of habitat fragmentation (black bars). Grey bars show articles including 'fragmentation' in the title. Dotted vertical lines represent publication of key papers by (A) Fahrig (2003) and (B) Lindenmayer & Fischer (2007) stressing the importance of separating composition from configuration.

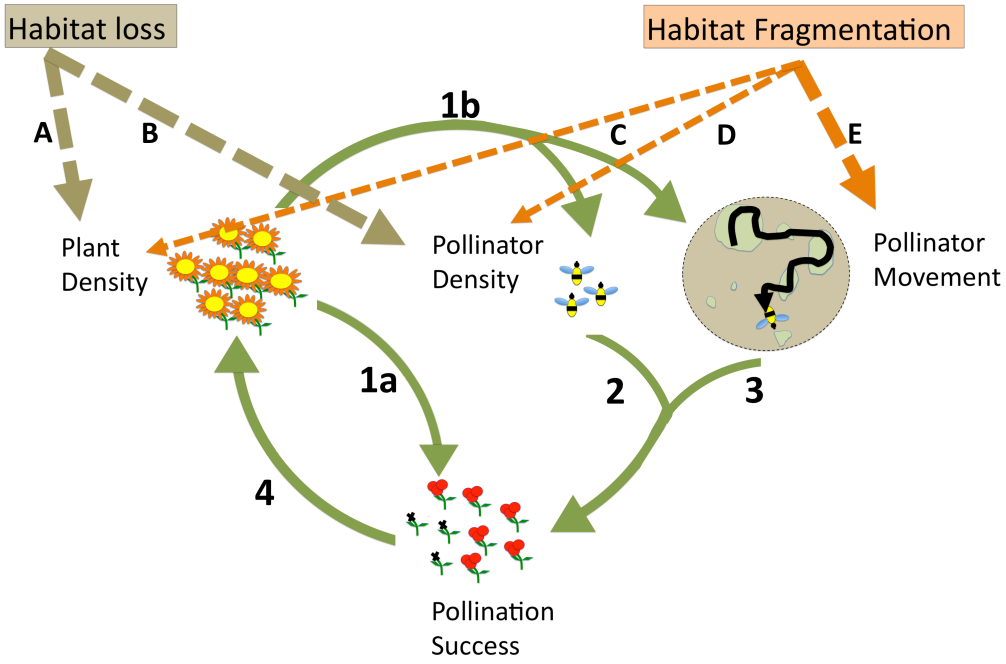

FIGURE 2.3. Conceptual model of the feedback loops involving the major components of pollination and the effects of habitat loss and fragmentation on each component. Dotted arrow thickness represents hypothesized effect strength. (1a) Plant densities directly affect pollination rates; reduced densities likely decrease pollen availability and therefore the likelihood of pollen transfer. (1b) Plant densities affect both pollinator densities, *via* behavioral and demographic processes, and pollinator movements. Pollinator densities (2) and pollinator movements (3) influence pollination success. Over the longer term, pollination success subsequently drives plant densities (4). Habitat loss can directly decrease plant (A) and pollinator (B) densities. Habitat fragmentation may increase or decrease plant (C) and pollinator (D) densities and also has been shown to influence pollinator movements (E). One hypothesis is that the number of different points where habitat loss and fragmentation may influence pollination systems, combined with the potential for feedback loops, may result in pollination services displaying high sensitivity to landscape changes.

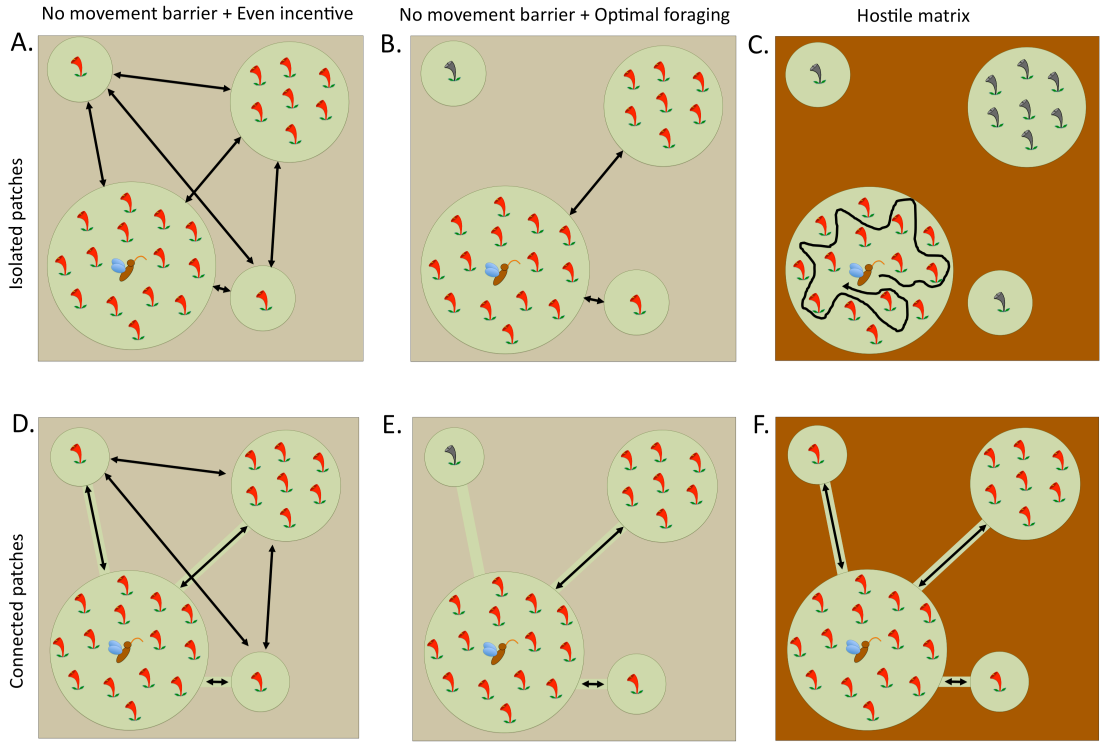

FIGURE 2.4. Schematic diagrams of the effects of matrix quality, incentive strength and connectivity on pollination. Suitable habitat (assumed to be the same for both the plant and pollinator) is shown in green with matrix types shown as either grey (no barrier to movement) or brown (extreme barrier to movement). Plants visited by pollinators are shown in yellow and unvisited plants are grey. Arrows represent pollinator movements. Panels A-C represent unconnected landscapes and D-F represent landscapes with patches connected by corridors. All landscapes have the same total amount of habitat. (A) Habitat patches are separated by a matrix that imposes no barrier to pollinator movement and the pollinator has even incentive to visit each patch because there is no cost to movement (i.e. pollinators move freely among all patches in the landscape). (B) Matrix imposes no barrier to movement, but pollinators make decisions according to optimal foraging. Pollinators visit patches according to distance/incentive trade-offs avoiding small remote patches. (C) Patches are imbedded in a 'hostile matrix' which prevents pollinator movement. The pollinator remains within a single patch. (D) Patches are connected by corridors, but the matrix imposes no barrier to movement and pollinators treat each patch as even incentive. Pollinators move between all patches as in A independently of actual habitat connections. Corridors play only a very limited role in situations with a highly permeable matrix. (E) Patches are connected, but pollinators make decisions according to optimal foraging. Movement trade-offs are the same as in B. (F) Patches are connected by corridors within a hostile matrix. Pollinators move along the corridors between patches. For graphical simplicity the matrix permeability we use here is artificially dichotomous (see Section VII). Complex interactions between pollinator behavior, landscape pattern, and matrix permeability are predicted to have strong implications for the importance of landscape fragmentation to pollination dynamics.

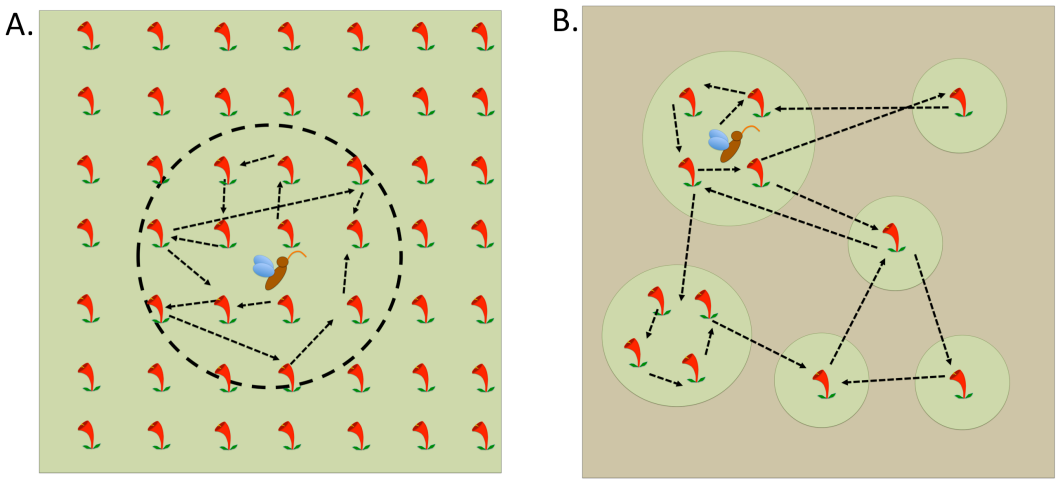

FIGURE 2.5. Diagrams representing the possibility for habitat fragmentation to increase outcrossing. (A) A landscape with high plant densities. Pollinator movements among flowers are shown by dotted arrows. The total area covered by the pollinator is shown by the dashed circle. This likely results in high levels of pollen delivery, but low rates of outcrossing. (B) Pollinator movements in a fragmented landscape with lower flower densities. The pollinator is forced to travel to more remote flowers in order to procure the same quantity of resources. This results in pollen movement among distant individuals that are less likely to be related, resulting in higher rates of outcrossing. It is important to note that the scenario shown in B requires a pollinator with high vagility and habitat generalization.

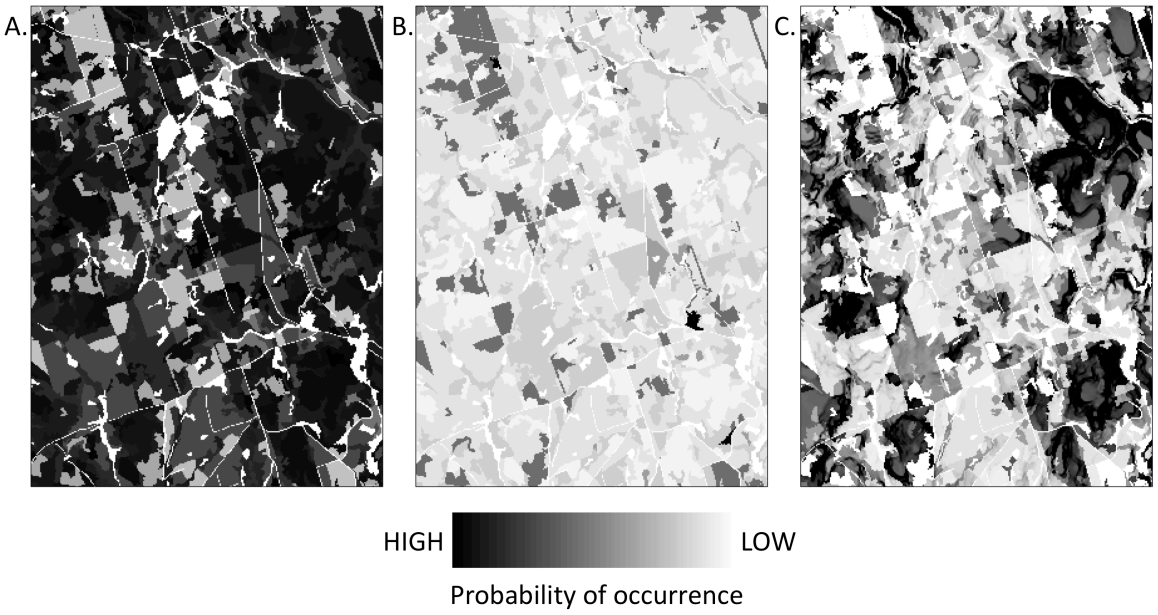

FIGURE 2.6. Three maps showing the same geographic area from the perspective of three different hypothetical pollinator species representing (A) a habitat generalist, (B) an early-seral forest specialist, (C) a late-seral forest specialist. In each map, dark shades indicate higher pollinator densities according to a species distribution model (SDM). Habitat amount, quality, patch size and connectivity all vary greatly within the same landscape depending on the organism.

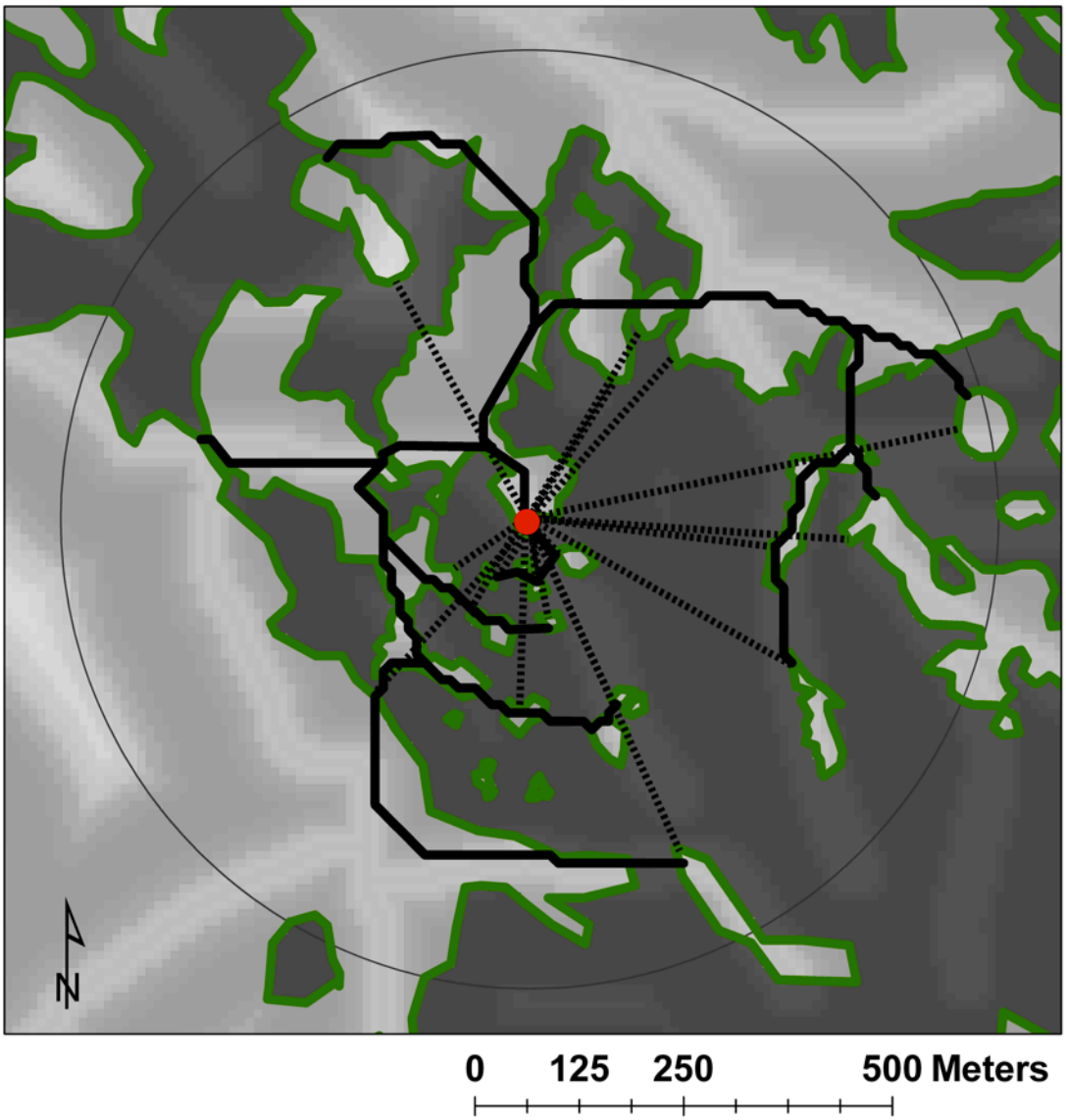

FIGURE 2.7. An example landscape showing the importance of using functional connectivity (solid lines) versus Euclidian distance (dotted lines) to determine connectivity of a focal patch (red central dot) at a spatial scale expected to be important to movements of Green Hermit hummingbirds (*Phaethornis guy*). Functional connectivity was quantified using actual hummingbird distributions as a response variable in a presence-only species distribution model (MAXENT; Phillips et al. 2006). The movement cost function (dark = high cost, light = low cost) was calculated as the inverse of occurrence probability. A least-cost path algorithm was used to determine the shortest paths. Patches of tropical forest are outlined in green (M.G. Betts & A.S. Hadley, unpublished data). In this case, portions of the landscape with very high functional connectivity tended to be forested riparian corridors.

TROPICAL DEFORESTATION ALTERS HUMMINGBIRD MOVEMENT PATTERNS

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3 TROPICAL DEFORESTATION ALTERS HUMMINGBIRD MOVEMENT PATTERNS

3.1 ABSTRACT

Reduced pollination success, as a function of habitat loss and fragmentation, appears to be a global phenomenon. Disruption of pollinator movement is one hypothesis put forward to explain this pattern in pollen limitation. However, the small size of pollinators makes them very difficult to track; thus, knowledge of their movements is largely speculative. Using tiny radio transmitters (0.25g), we translocated a generalist tropical 'trap-lining' hummingbird, the Green Hermit (*Phaethornis guy*), across agricultural and forested landscapes to test the hypothesis that movement is influenced by patterns of deforestation. Although we found no difference in homing times between landscape types, return paths were on average 459±144m (± s.e.) more direct in forested than agricultural landscapes. In addition, movement paths in agricultural landscapes contained 36±4% more forest than the most direct route. Our findings suggest this species can circumvent agricultural matrix to move among forest patches. Nevertheless, it is clear that movement of even a highly mobile species is strongly influenced by landscape disturbance. Maintaining landscape connectivity with forest corridors may be important for enhancing movement, and thus in facilitating pollen transfer.

3.2 INTRODUCTION

Recent research shows global declines in plants and associated pollinators (Biesmeijer et al. 2006), sparking concerns about a widespread pollination crisis. The causes of these declines remain obscure, but habitat loss and fragmentation are expected to be primary drivers since pollen is often limited in fragmented landscapes (Aguilar et al. 2006, Steffan-Dewenter and Westphal 2008). Unfortunately, the specific mechanisms for pollen limitation remain largely unknown. Three hypotheses have been forwarded to explain pollen limitation as a function of habitat loss and fragmentation. First, landscape disturbance may negatively affect plant abundance, density and health, thereby reducing

the total amount of pollen available for transfer (de Blois et al. 2002). Second, the abundance, distribution, and diversity of pollinators upon which plants depend may be reduced by landscape disturbance (Steffan-Dewenter and Westphal 2008). Finally, disturbance may restrict the movements of pollinators, thus reducing their effectiveness in pollen transfer (Tewksbury et al. 2002). Despite the potential for direct effects of animal movement decisions on pollination, the pollinator movement hypothesis has received little attention due to the inherent difficulties in tracking small pollinators (Ghazoul 2005).

Previous work has shown continued persistence of several hummingbird species in fragmented tropical landscapes (Stouffer and Bierregaard 1995). Taken superficially, this could imply that plant species reliant on hummingbird pollinators should show minimal pollen limitation; however, hummingbird persistence at the landscape scale does not imply that all patches in a landscape will be visited frequently, or that inter-patch pollen transfer will occur. Pollen transfer is determined by whether landscapes facilitate or impede pollinator movements between resource patches (i.e., its 'functional connectivity'; Bélisle 2005). Indeed, varying costs associated with different landscape elements (e.g., patches, matrix, corridors; Forman 1983) are hypothesized to affect animal movement decisions (Lima and Zollner 1996).

Experimental manipulations, such as translocations and precise tracking methods, are thought to provide meaningful measures of functional connectivity; the rates and paths of animal return to territorial patches provide measures of landscape resistance (Bélisle 2005). Our research capitalized on recent advances in miniaturization of animal tracking technology (e.g., Wikelski et al. 2006) that, along with a translocation approach, allowed us to test the hypothesis that hummingbird movement is altered by tropical deforestation.

We investigated the effects of tropical forest conversion to agriculture on movements of the Green Hermit (*Phaethornis guy*), a generalist forest 'trap-lining' species. We selected a trap-liner because they acquire necessary resources from isolated nectar-rich flowers

over relatively large spatial scales, a strategy which precludes territoriality (Stiles 1975). We chose a generalist species because changes in its movements will probably have broader ecological impacts than in the case of more specialized pollinators (Ghazoul 2005). Generalist pollinators affect a large number of plant species, particularly pollinator specialized plants which often depend exclusively on generalist pollinators for pollen transfer (Bascompte et al. 2006). Green Hermits are forest-dependent, but persist in fragmented landscapes, making them ideal for comparing movements between altered and intact landscapes.

We compared the functional connectivity of primarily agricultural versus forested landscapes. If deforestation impedes hummingbird movements, we expected longer homing times and/or limited homing success in agricultural relative to forested landscapes. Second, if hummingbirds take detours and avoid crossing open pastureland while homing, movements through agricultural landscapes should be longer and less direct than those taken through forest. Third, we expected homing paths in agricultural landscapes to be characterized by greater forest cover in comparison to the most direct routes to capture locations.

3.3 METHODS

3.3.1 Study site

We conducted the study at the Organization for Tropical studies, Las Cruces Biological Station, Costa Rica (8^{o}47N, 82^{o}57W). The site contains a 235 ha reserve comprised of primary and old secondary forest. The surrounding agricultural matrix was previously forested, but now is dominated by pasture and shade coffee plantations. Remaining fragments of Pacific premontane humid forest (1-82ha) and forested riparian corridors (10-40m wide) are scattered throughout this agricultural landscape.

3.3.2 Telemetry and translocations

We captured 19 Green Hermits (8 male, 11 female) January 30 –March 9, 2008 and fitted them with radio-telemetry units (0.25g, Blackburn Transmitters, Fig. 3.1). The relatively large size of this species (5.8±0.09g), made it a logical first test of using telemetry to monitor hummingbird movements. We used eyelash glue to attach transmitters to plucked bare skin on the lower backs of birds. Transmitters fell off very rapidly (~2 weeks) once the feathers began to re-grow. Hummingbirds appeared to have no difficulty flying with the radio-tags; we observed no behavioral differences between tagged and untagged individuals. In one instance, we observed a tagged female chasing off an untagged individual during a territorial dispute.

We translocated 10 hummingbirds through continuous forest and 9 across agricultural landscapes. We maximized differences between forested and agricultural treatments by translocating birds across agricultural landscapes with <50% residual forest. Hummingbirds were transported 340m-1500m, providing a range of distances that allowed us to test the effect of scale on homing efficiency. Translocations were conducted between from 0600 and 1500; no results were influenced by time of day ($p>0.4$). We placed hummingbirds in cloth bags and transported them by foot or vehicle depending on terrain. Release points were dictated, to a certain extent, by roads and trails to minimize handling time (<40min). We alternated translocation distance (<1000/>1000m) and landscape type (agriculture/forest).

We recorded homing times for returning individuals and the movement paths they used. We followed birds as closely as possible on foot (<200m) using two teams with radio receivers and handheld Yagi antennae. Bird locations were recorded whenever a position could be determined to within 50m (mean=8 points/bird, range 4-14; short-distance translocations had fewer locations). Based on trials under optimal conditions with known transmitter distances, we assumed that a bird was within 50m whenever signal strength was 0.4 (gain <1/2). A bird was considered to have successfully homed when it was relocated within 50m of the capture location.

3.3.3 Analysis

We calculated the effects of landscape type on home time, difference in path length, and fractal dimension using Generalized Linear Models with a Gaussian distribution. We used fractal dimension to measure path tortuosity (i.e., the degree of twisting and turning). Fractal dimension (D) was calculated as: [$D = \log(n) / (\log(n) + \log(d/L))$, where L = total path length, d = length of line segment, and n = number of segments]. Number of segments was included in all GLMs containing D in order to account for the different number of spatial locations collected for each path. To determine if birds selected forest when moving through agricultural landscapes, we calculated the proportion of forest within 30 and 100m diameter buffers around the movement paths of each individual (i.e., 'observed') and around the shortest distance between capture and release points (i.e., 'available'). The 30 m buffer reflects the average width of linear forest strips within study area agricultural landscapes. Because our forest data were not normally distributed, we tested for differences between observed and available proportions of forest using Exact Wilcoxon signed rank tests. We used R (version 2.7.1) for all statistical tests. In all analysis, we report mean differences±s.e.

3.4 RESULTS

All but one individual homed successfully within 4 hours of release, even over translocation distances up to 1500m. The single individual that failed to return home (translocated 1300m across an agricultural landscape) was excluded from all analyses. We detected no difference in homing times between agricultural and forested landscapes (difference in means=9.7±22min, F=0.73, N=18, p=0.71, Fig. 3.2a). However, homing paths of birds in agricultural landscapes were 459±144m longer (F= 10, N=18, p=0.006, Fig. 3.2b, [forest 153±70m, agriculture 544±129]) and more tortuous (0.230±0.013, F= 9.6, N=18, p=0.007, [forest 1.12±0.04, agriculture 1.4±0.08]) than those through contiguous forest.

Hummingbirds tended to associate with forest remnants when homing through agricultural landscapes. Movement paths of homing individuals contained 36± 4% more forest than if they had taken the most direct route (30m buffer; W=0, $p<0.01$, N= 8). At the 100m buffer scale, paths contained 68± 4% more forest (W=0, $p<0.01$, N= 8).

3.5 Discussion

Green Hermits appear to have excellent homing capacities, even in heavily deforested landscapes. Contrary to our expectations, and unlike several previous translocation studies (e.g., Bélisle et al. 2001), homing times did not depend on whether landscapes were primarily forested or agricultural. In both landscape types, birds returned within 4 hours even when translocated up to 1500m. This is congruent with previous studies showing relatively high vagility of a *Phaethornis* hummingbird species (Moore et al. 2008).

However, the paths selected by hummingbirds to traverse intervening landscapes revealed that deforested gaps alter movement pathways. In agricultural landscapes, birds moved longer distances and took more circuitous routes than in forested landscapes. Overall, movement paths were strongly biased toward areas with higher forest cover. Though this does not represent the extreme gap crossing avoidance shown by some other tropical species (Stratford and Stouffer 1999, Moore et al. 2008), it does show that even highly mobile species can be influenced by fragmentation. An agricultural matrix may increase the vulnerability of hummingbirds to predators at forest edges. Animal movements are often influenced by perceived risk of predation even if the probability of mortality is low (Lima and Zollner 1996).

We show that even a generalist species with high vagility avoids crossing open matrix in favor of longer forested detours. Asymmetric coevolution of pollination networks has resulted in the reliance of many plants on generalist pollinators as their sole source of pollen (Bascompte et al. 2006). Changes in movement patterns as a function of landscape

context could thus have profound impacts on pollen movement (Steffan-Dewenter and Westphal 2008) and therefore the persistence of many plant species.

Our work adds to a growing body of evidence for the importance of remnant forest strips and riparian buffers (i.e., corridors) in highly modified landscapes (Tewksbury et al. 2002, Hawes et al. 2008). Maintenance of forest along hedgerows or streams will likely facilitate inter-patch movements and should be important for pollen transfer events. We predict that fidelity to linear forest habitats by hummingbird pollinators could 'scale up' to result in fragmentation effects on plant demography that are independent of the detrimental influence of habitat loss (Fahrig 2003).

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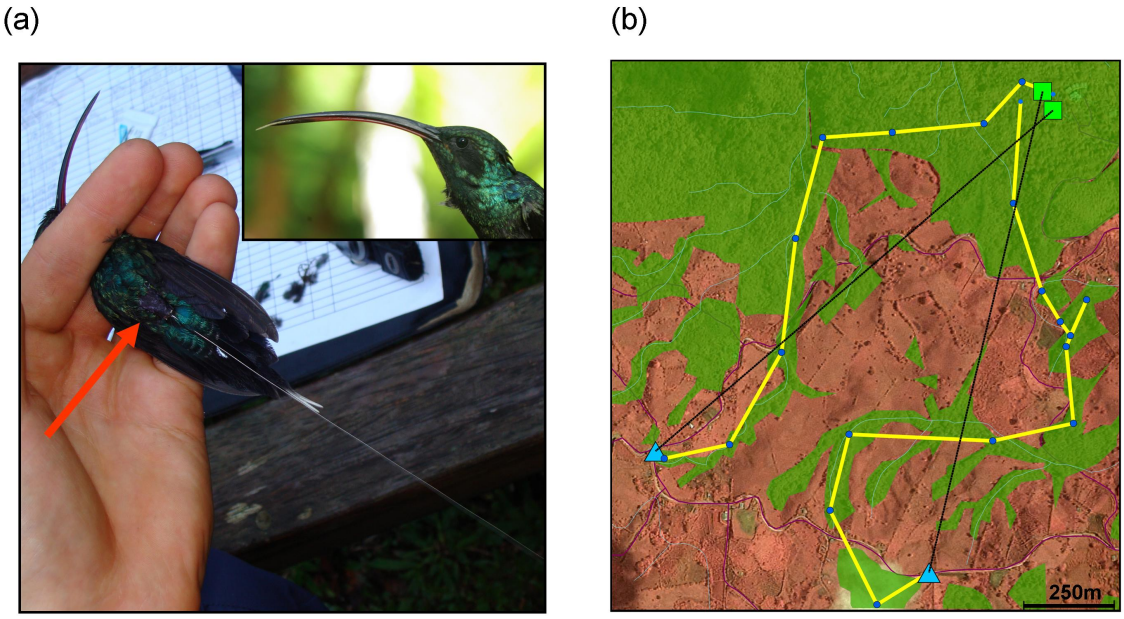

FIGURE 3.1. (a) An adult Green Hermit (*Phaethornis guy*; inset) and the same species with a transmitter attached for monitoring movements. (b) An example of two hummingbird movement paths through agricultural landscapes. Movement paths are shown in yellow with telemetry locations in blue. Direct line distances between release (blue triangles) and capture locations (green squares) are shown in black. Forested areas are in green, agriculture in brown. Photo credits: M. Betts (a, inset), J. Miller (a).

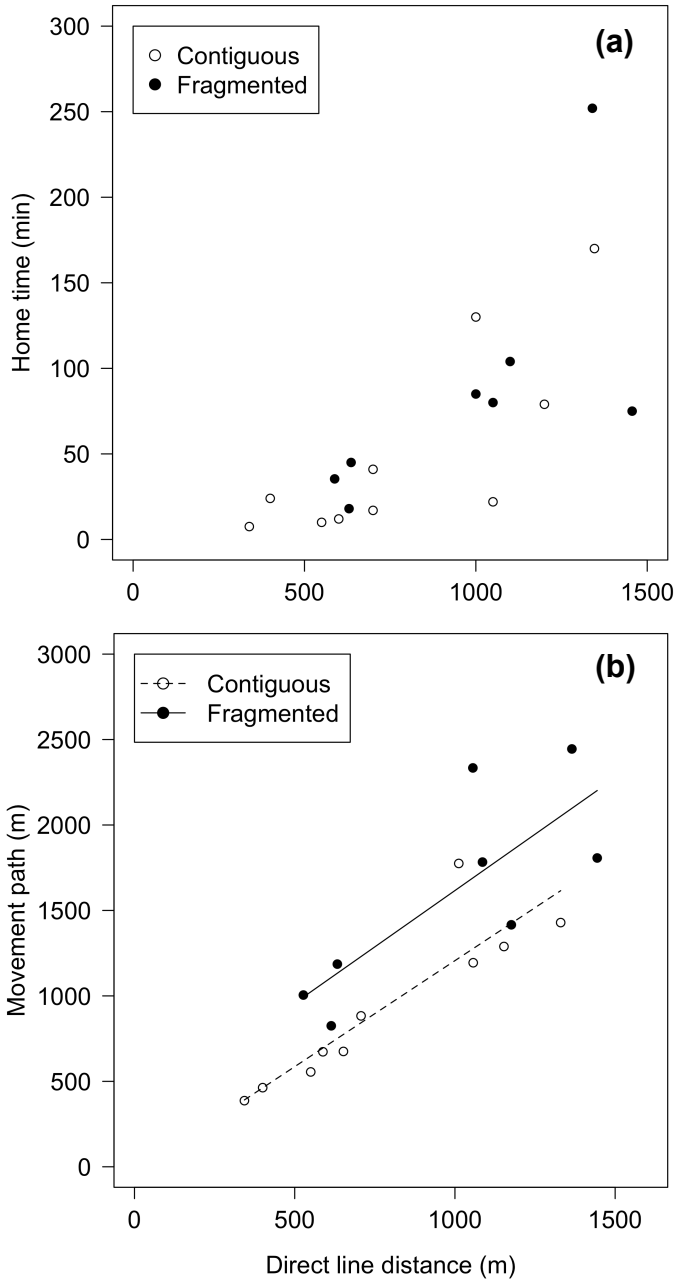

FIGURE 3.2. (a) Homing times for 18 Green Hermits translocated across agricultural (fragmented) and forested (contiguous) landscapes. (b) The directness of homing movements for birds translocated across agricultural (fragmented) and forested (contiguous) landscapes.

FOREST FRAGMENTATION, BUT NOT LOSS AFFECTS POLLINATION IN A TROPICAL UNDERSTORY HERB *HELICONIA TORTUOSA*

Adam S. Hadley, Sarah J.K. Hadley, W. Douglas Robinson, W. John Kress, and Matthew G. Betts

4 FOREST FRAGMENTATION AFFECTS POLLINATION OF A TROPICAL UNDERSTORY HERB *HELICONIA TORTUOSA*

ABSTRACT

Loss and fragmentation of native vegetation cover are thought to be major drivers of widespread declines in pollination success. However, the specific mechanisms by which these landscape changes are driving declines remain unknown; little is understood about the relative contribution of landscape composition versus configuration on disruption of pollination services. We tested the relative importance of landscape composition versus configuration on the reproductive success of *Heliconia tortuosa*, a hummingbird-pollinated forest herb, near Las Cruces, Costa Rica. Hummingbirds in this system have been shown to avoid crossing non-forested matrix, suggesting a potential mechanism for independent configuration effects on pollen limitation in disturbed landscapes. We used a stratified random sampling design to select sites across orthogonal gradients in patch size, amount of forest, and elevation (N=37 patches [287 plants]). We examined presence of pollen tubes, presence of fruit, proportion of successful fruits and proportion of seeds produced. Using linear mixed models with 'patch' as a random effect, we modeled the effects of local site, composition, and configuration variables. We statistically controlled for the influence of local site and composition variables when testing for configuration effects. Our work provides evidence for an effect of habitat fragmentation on *H. tortuosa* seed set, but not other aspects of plant reproduction such as pollen tube growth or fruit set. Increasing log-patch size had a positive effect on proportion of seeds produced independent of forest amount. We found little support for landscape composition models suggesting that configuration of the remaining forest may be more important to heliconia reproduction than the amount of forest in the landscape. We found that the relative abundance of pollinators was also configuration dependent. Log patch size had a positive effect on the abundance of pollinators independent of forest amount. We hypothesize that differences in pollen quality resulting from changes in hummingbird movements and/or relative abundance are driving landscape configuration effects on heliconia reproduction.

4.1 Introduction

Pollination services are declining (Eckert et al. 2010). A major driver of pollination declines is hypothesized to be antropogenic changes in the amount and distribution of native habitats across landscapes (Aguilar et al. 2006). However, which landscape attributes (e.g., habitat amount, connectivity, patch size) or what components of the pollination system (e.g., pollinator density or movement, plant demography) drive frequently observed pollination failure remain unclear. Turner (1989) defined the two major elements of landscape structure as composition and configuration. Landscape composition combines the type and amount of habitat or cover types within a landscape, while landscape configuration reflects the spatial pattern of landscape elements (Turner 1989). Subsequently, 'habitat loss' refers to changes in landscape composition and 'fragmentation per se' refers to the spatial configuration of remaining habitat, independent of the amount of habitat within the landscape (Fahrig 2003).

Habitat loss and fragmentation may influence pollination through three main components: pollinator density, pollinator movement, and plant demography (Ghazoul 2005, Kremen et al. 2007). First, landscape disturbance may negatively affect plant abundance, density, and health (de Blois et al. 2002), thereby reducing the total amount of pollen available for transfer. Second, the abundance, distribution, and diversity of pollinators upon which plants depend may be reduced by landscape disturbance (Steffan-Dewenter and Westphal 2008, Winfree et al. 2009). Finally, disturbance may restrict the movements of pollinators (Tewksbury et al. 2002) or alter their behavior under differing foraging contexts (Chittka and Schurkens 2001), thus reducing their effectiveness in pollen transfer. This reduction in pollen transfer effectiveness in disturbed landscapes can result from two factors associated with pollen delivery (Aizen and Harder 2007). Quantity limitation occurs when the stigmas receive too few pollen grains to maximize ovule fertilization. Quality limitation occurs when flowers receive low quality pollen (i.e. self or closely related pollen grains from flowers in close proximity). Quantity limitation is restricted to the lowest levels of pollen delivery, but quickly becomes less important as pollen loads increase. Quality limitation can still have effects through the entire range of

pollen quantity delivered (Aizen and Harder 2007); a plant can still be quality limited at both low and high levels of pollen delivery. Low quality pollen reduces seed set, germination, and subsequent plant growth in a large number of plant species (Husband and Schemske 1996). Inbreeding depression is also affected by pollen quality and its effects can extend throughout the lifecycle of the progeny (Charlesworth and Charlesworth 1987).

Trying to separate the effects of habitat loss and fragmentation in ecological research has proved difficult since landscape composition and configuration are almost always confounded (Fahrig 2003); landscapes with large amounts of habitat are typically un-fragmented, while landscapes with low amounts of habitat usually are also those having small, unconnected patches (Fahrig 2003). To draw inferences about the independent effects of fragmentation, researchers must separate the confounding effects either statistically or through experimental design.

Both changes in composition and configuration independently have the potential to influence pollination dynamics by directly affecting pollinator or plant densities and altering pollinator behavior (Hadley and Betts 2012). Changes in composition versus configuration could have dramatically different effects on pollination. Understanding the mechanisms behind apparent landscape-driven pollination declines is thus integral to successful conservation measures and maintenance of ecosystem services. In a recent review, Hadley and Betts (2012) found that only six of 303 studies considering the influence of landscape change on pollination separated the effects of habitat loss from fragmentation. Many articles measured configuration metrics (e.g., patch size, isolation, edge), but only five empirical studies and one simulation study successfully distinguished changes in landscape configuration from those of composition. This suggests that while landscape changes appear to be having widespread negative effects on pollination, the specific mechanisms (e.g., habitat loss or fragmentation) remain elusive.

In addition to difficulties in separating effects of composition from those of configuration, landscape-scale pollination studies have proved complicated due to issues relating to inadequate replication, choice of scale, and definitions of habitat or matrix. Landscape-

scale studies frequently encounter issues of small sample size and low replication, pollination studies are no exception. A recently meta-analysis of studies examining effects of human disturbance on plant-pollinator interactions found that half of the studies examined only a single disturbed site compared to a single undisturbed site (Eckert et al. 2010). In the absence of large-scale experimental manipulations, extensive replication across ecological gradients was suggested as the best way to fix this issue in future studies (Eckert et al. 2010).

Decisions on the spatial scale of research need to be justified in biological terms relating to the question of interest rather than logistical constraints (e.g., Kremen et al. 2002, Holzschuh et al. 2010). Similarly, most studies use anthropogenic definitions of changes in composition and configuration (e.g., forest/non-forest, native grassland/crop fields). While these delineations often have important management and conservation implications, they may not reflect strict habitat/non-habitat designations for the species of interest. Defining habitat from the perspective of the study species and examining how the landscape changes using this species-centered approach can reveal effects that might not be otherwise apparent (Betts et al. 2006). Defining habitat and matrix is also complicated in pollination studies because the habitat for the pollinator and the plant are not necessarily the same. Pollinators' use of matrix between patches of native habitat can have profound impacts on within-patch dynamics (Jules and Shahani 2003).

The potential for landscape change to affect populations through changes in composition and configuration has been expressed as four competing hypotheses with differing implications for habitat loss and fragmentation (Betts et al. 2006). Here we apply these hypotheses to pollination success as opposed to 'populations' in order to develop a framework to test the mechanisms behind landscape-level pollination declines.

The first hypothesis is the *local* or *random-sample hypothesis* (Haila 1983). Under this scenario small patches are simply random samples of larger patches; therefore only factors at the local extent or the level of individual plants are important in determining pollination success. If this is the case, we do not expect to see any influence of either

fragmentation or habitat loss on pollination success, rather pollination success should be driven primarily by local-scale factors.

The second hypothesis is the *landscape composition hypothesis* (Fahrig 2003) where the amount of habitat in the landscape is important to pollination at scales larger than the individual plants. Under this hypothesis we expect pollination failure to increase with decreasing amounts of habitat in the landscape, regardless of configuration. This hypothesis is most likely to be the case if pollination success depends primarily on either the abundance of available flowers or pollinators at broader spatial scales. In general, reducing numbers of both plants and pollinators would result in lower pollen availability and fewer vectors to move pollen through the landscape, thereby reducing pollination success. Landscape composition could also affect pollination through matrix quality (Jules and Shahani 2003). High quality matrix containing alternative flower sources could allow pollinators to persist in landscapes with low amounts of native habitat by providing options for resource supplementation in the matrix.

The *landscape fragmentation hypothesis* (Villard et al. 1999) anticipates that after controlling for effects of habitat loss, pollination failure should increase in a linear fashion with increasing fragmentation. Fragmentation effects per se can result through edge effects, differences in connectivity and patch size differences (Fahrig 2003). If either plant or pollinator densities differ depending on landscape configuration or if pollinator behavior, particularly movement, is influenced by landscape pattern, then it is likely that pollination success will vary.

The *fragmentation threshold hypothesis* (Andren 1994, Betts et al. 2006) states that landscape configuration is only important below some critical habitat amount. Under this hypothesis, we predict that reduced pollination should only occur in highly fragmented landscapes with low amounts of habitat cover. Support for this hypothesis is most likely if small gaps pose no obstacle to pollinators but large gaps reduce movement (Gillies and Clair 2008). An additional special case of the fragmentation threshold hypothesis applies if matrix quality is only important when patches drop below a certain size and/or amount

of native habitat in the landscape. Resource supplementation from the matrix may only happen below certain native habitat thresholds and, therefore, be context dependent.

We test these four landscape change hypotheses by conducting a large-scale mensurative experiment (Hurlbert 1984) designed to disentangle the effects of local site characteristics, landscape composition, and landscape configuration on pollination of an understory tropical forest herb *Heliconia tortuosa*. We attempt to determine the components of the pollination system (i.e., pollinator density, pollinator movement, and plant demography) that are driving any landscape affects we detect. We investigate the importance of scale at four different extents in this pollination system. In addition to testing typical anthropogenic composition measures (i.e., amount of mature tropical forest), we use an organism-based habitat model to quantify the amount of *H. tortuosa* habitat available. We also quantify matrix resource availability at two spatial extents. To our knowledge this is the first attempt to disentangle the effects of composition and configuration in a tropical pollination system.

4.2 METHODS

4.2.1 Study region

The study was conducted in a (~31000 ha) area of Coto Brus Canton in southern Costa Rica (8° 47' 7" N, 82° 57' 32" W) surrounding the Organization for Tropical Studies Las Cruces Biological Station. The study region is composed of 43.2% Pacific premontane tropical forest and spans an elevation gradient from ~300 to 1500 m.a.s.l. The agricultural matrix was previously forested, but now is dominated by pasture (~80% of matrix) and shade coffee plantations. The majority of land clearing occurred prior to 1990 (Sánchez-Azofeifa et al. 2001) , and remaining forest patches span a range of sizes from <1 to >1000 ha across a gradient in forest amount from 1 – 99 % forest within one kilometer (Fig. 4.1).

4.2.2 Study species

Heliconia tortuosa is an understory forest heliconia that flowers from January-June with a peak around March in the study area. *H. tortuosa* can reproduce vegetatively by clonal growth and clones can be quite old (> 40 years W.J.K pers. com.). This species is pollinated primarily by long-billed, traplining hummingbirds, particularly hermits, due to its long curved corollas (Stiles 1975). *H. tortuosa* requires pollinator visits for successful sexual reproduction and is thought to be partially self-incompatible. Kress (1983) found that *H. tortuosa* produced 50% more pollen tubes when supplementally pollinated with outcross pollen than with self-pollen. *H. tortuosa* produces an inflorescence that typically has between six and ten bracts (Berry and Kress 1991). Each bract can have 10 - 30 flowers which open sequentially with less than one flower/bract/day (Fig. 4.2). The flowers are 'single day blossoming' meaning that each flower is only open for a single day before it abscises (Kress 1983). A single inflorescence may produce hundreds of flowers in a season, but typically has less than three open per day. It takes approximately two months following successful pollination for a mature fruit to be produced (Kress 1983), but successful ovules begin to swell within a week following pollination. Each fruit can contain one to three seeds, which are thought to be dispersed primarily by birds (Berry and Kress 1991).

4.2.3 Study design

Changes in composition and configuration are confounded in our system. If we randomly sample forest patches within the study area, patch size and amount of forest within 1000 m are highly correlated ($r^2 > 0.7$). Since it is not logistically feasible to conduct manipulative experiments at the landscape scale in this region, we conducted a mensurative experiment in which we independently varied composition (forest amount) and landscape configuration (forest patch size; sensu: Betts et al. 2006). We used a stratified random sampling design so that samples represented the full range of variation in patch size and amount of forested area ('forest amount') within 1000 m of the sample site. For the purposes of study design we chose '1000 m' as we expected this to be a key

range within which pollinators are moving based on experimental translocation data and passive movement observations (Hadley and Betts 2009).

Forest patches were considered distinct when they were separated by at least 30 m from the nearest forested area. For the purpose of patch selection we defined two patch size categories (small <5 ha, large >40 ha), and two forest amount categories (low <30 % and high >40 % forest). We then randomly selected patches falling within each of these specifications. Since patch size and amount of forest could also be positively correlated with elevation due to land clearing practices in the area, we also stratified across two elevation bands (low 900-1199 m.a.s.l. and high 1200-1500 m.a.s.l.; 900-1500 m represents the range of *H. tortuosa* within the study area). This increased the likelihood that poorly represented combinations of patch size, forest amount, and elevation were included within our sample. Forty suitable patch/landscape combinations were randomly selected using these criteria; permission for access was denied in three instances leaving 37 patches (Fig. 4.1). The correlations in our sampled patches were as follows: patch size/amount of forest r^2=0.34, patch size/elevation r^2=0.19, and amount of forest/elevation r^2=0.18. In 2010 we sampled 34 patches (3 suffered understory disturbance from cattle or had the sample plants destroyed) and in 2011 understory disturbance, reduced patch access and a conflicting experiment rendered additional patches unusable reducing the sampled patches to 25.

4.2.4 Scales of interest

Given some uncertainty in the appropriate scale, we tested multiple extents to reduce type-two error. Based on earlier movement work with Green Hermits (*Phaethornis guy*) we predicted that hermits were spending a majority of time within a relatively small area (<500 m), but are also likely to be making longer distance movements (<1000 m) and be familiar with the landscape at a larger extent (<2000 m) (Hadley and Betts 2009). Since we do not yet have detailed knowledge of the most pertinent scale, we investigatedthe importance of composition metrics within these three radii. We also examined the

importance of microhabitat or 'local'-scale factors at the site of each focal plant (see 4.2.7).

4.2.5 Landscape composition

Forest amount.- Since both *H. tortuosa* (Berry and Kress 1991) and its most common pollinators (Borgella et al. 2001) are forest species, we used GIS to quantify the amount of forest in the surrounding landscape as a measure of landscape composition. We currently lack the data to construct more detailed species-specific habitat maps for all of the pollinator species involved, but we expect that 'forest' should be a coarse estimate of amount of habitat available for the hummingbird pollinators.

Heliconia habitat amount.- To generate a species-specific view of habitat suitability within the study area, we constructed a *H. tortuosa* species distribution model (SDM). This is relevant to heliconia fitness since it provides an index of conspecific flowering densities at the landscape scale. *H. tortuosa* flowers provide a relatively large quantity of nectar and represent a substantial resource for hummingbirds (Stiles and Freeman 1993). Therefore, the distribution of heliconia flowers should be relevant to hummingbird movement behavior and distributions. We used presence data obtained from locations of 160 flowering *H. tortuosa* plants across our study area collected during February-March 2010. We used Maximum Entropy Modeling (MaxEnt; Phillips et al. 2006) to build a distribution model that predicted the presence of flowering as a function of Landsat reflectance bands and other environmental features. MaxEnt is thought to be one of the most efficient approaches to creating SDMs using presence-only data (Elith et al. 2011). MaxEnt assesses the probability of presence in a given cell on the basis of environmental features in that cell. Our environmental variables included eight reflectance bands from a 2003 Landsat image of the study region (NASA Landsat Program 2003, Shirley et al. In review). We used 2003 since it represented the most recent cloud-free image and also avoided any issues involving the Landsat 7 scan line correction (SLC) failure (NASA Landsat Program 2003). We feel that since the majority of landscape change occurred before 2003 and cloud-free areas of the 2011 image were highly correlated with the equivalent areas of the 2003 image ($r^2 = 0.73$), this older image is still suitable. We also

included in our models three topographic variables (elevation, slope, aspect) and some measures of landscape context (distance to stream, distance to edge, forest/non-forest) derived from GIS layers of the study area. We used 20 X 20 m cells and gathered the environmental data for each raster cell. We performed 10-fold cross-validation, and calculated the area under the curve of the receiver-operator plot (AUC) as a measure of matching between our model results and the heliconia presence records (Training AUC = 0.967, Test AUC = 0.9532, Standard deviation = 0.0119; Fig. 4.3). The variables with the highest predictive contributions were elevation and forest (Appendix B). To quantify flowering *H. tortuosa* habitat we summed heliconia suitability 'probabilities' for all of the pixels within the scales of interest (sensu: Betts et al. 2006).

Matrix resources.- In March 2012 we surveyed flower resources in the matrix. We counted the number of ornithopilous flowers that could be observed from roads in the study area. We sampled along roads for logistical reasons, but feel that it represents a useful assessment of resources available to hummingbirds outside of forest patches; most of the flowering resources in the matrix were domestic species and usually were located within sight of roads. Areas far from roads were almost exclusively pastureland and devoid of suitable flowers. We expect that despite the fact that resource sampling was not conducted in the same year as the pollination work, it should still provide valuable information, since the majority of the species sampled are long lived with long flowering periods. Low turnover in landowners insures a high degree of temporal autocorrelation in the abundance of flowering domestic plants across the study landscapes.

4.2.6 Landscape configuration

We chose forest patch size as our measure of landscape configuration. Patch size is the most commonly investigated landscape variable in pollination studies (Chapter 2, Hadley and Betts 2012), yet the actual contribution of patch size to changes in pollination has typically been confounded by simultaneous compositional changes. We used log-patch size because we expect the biological effects of increasing patch size to be an asymptotic. We chose not to investigate isolation per se since most traditional measures of isolation are highly correlated with habitat amount on the landscape (Bender et al. 2003).

Structural connectivity measures were also avoided since they are not necessarily reflective of actual functional connectivity (Bélisle 2005).

4.2.7 Plant selection

In each of forest patch we sampled from the patch edge beginning at a randomly selected point from within 500 m from an access point. Plant selection was opportunistic; the first five *H. tortuosa* plants with inflorescences that we encountered searching outwards from the random point were selected and uniquely labeled. If five flowering *H. tortuosa* were not immediately located, the patch was searched for up to three person-hours to locate additional plants. In 2010 we sampled 197 plants and in 2011 ninety new plants were sampled for a combined total of 287 plants in 37 patches.

For each plant we recorded data on plant size and local environmental features to allow statistical control for possible site level confounds. We controlled for plant vigor (Knight et al. 2005) using plant height (i.e., from ground to top of the tallest leaf petiole) and the number of bracts on the flowering inflorescence. Both are thought to be important indications of heliconia age and vigor (Bruna and Kress 2002). We sampled the local flowering community within 20 m of each focal plant as a measure of conspecific and heterspecific flower densities. For conspecific density we counted all flowering *H. tortuosa* within 20 m. As an index of heterospecific densities, we counted the number of 'ornithophilous' species and the total number of ornithophilous flowers within 20 m. We also quantified distance to the nearest edge, distance to the nearest stream, and the elevation at the plant location.

4.2.8 Pollinator sampling

We sampled hummingbirds in a subset of the patches in February-March 2011. We randomly selected 14 patches representing the extremes in the patch size/amount of forest gradient (i.e., small patches surrounded by low amounts of forest and large patches surrounded by a high amount of forest). We sampled the extremes since they represent the conditions where we would expect any differences resulting from the combined

effects of habitat loss and fragmentation to be greatest (Zitske et al. 2011). We captured hummingbirds using ten, 12 m mistnets opportunistically placed in front of ornithophilous flowers within each patch. Area sampled by net arrays was consistent across patch sizes (sampling area versus patch size correlation: r^2 = -0.250, p = 0.39, 0.3±0.21ha [mean±SD]). Captures were conducted between 0530 and 1230. We marked the top of the head of all hummingbirds that were captured with unique combinations of dots using colored nail polish so that we could identify them as recaptures. Each netting site received three visits separated by a minimum of four days. Order of visits was randomized. We examined the capture rates of Green Hermits (*Phaethornis guy*) since they appear to be a primary visitor of *H. tortuosa* in the study area (A.S.H. pers. obs., 7/12 visits to a clump of *H. tortuosa* within four hour observation period). In addition to Green Hermits, we examined the total captures of all hummingbird species thought to be legitimate pollinators of *H. tortuosa* (i.e., those observed to touch the reproductive parts of heliconia flowers when feeding). These include both hermits (Phaethorninae) and non-hermits with long and/or curved bills that forage in a hermit-like manner (Stiles and Freeman 1993).

4.2.9 Measures of pollination success

We used three different measures of pollination success, each representing successively higher levels of reproductive information.

Pollen tubes.- H. tortuosa flowers abscise within 24 hours of opening. We removed day-old flowers from plants and collected the styles according to Kress (1983). The styles were fixed in formalin - acetic acid - alcohol (FAA) solution for 24 hours and then transferred to 90% ethanol for storage. We processed the styles using a series of washes: 1. Styles were soaked in distilled water for 24 hours to remove any remaining FAA solution, 2. Styles were soaked in 8 N sodium hydroxide (NaOH) to soften the tissue, 3. A second distilled water rinse was used to remove remaining NaOH, 4. We stained the styles in 0.01% decolorized aniline blue for > 3 hours. We mounted the styles on slides by crushing them under a coverslip. The prepared styles could then be examined examined under epi-fluorescence microscopy (according to: Kress 1983). Successful

pollen tubes contain callose which, when stained with aniline blue, are visible under ultraviolet light (Kearns and Inouye 1993). We recorded the presence/absence of pollen tubes in each style. We examined 530 styles from 270 plants. When possible we collected two flowers from each plant. Heliconia require pollinator visitation in to have successful pollen tubes, but pollen tubes can grow with both self and outcross pollen (Kress 1983). However, the presence of successfully germinated pollen tubes does not necessarily guarantee the production of fruits or seeds (Ramsey and Vaughton 2000).

Fruit set.- After the end of flowering, but before fruits fully ripened, we covered inflorescences with mesh bags. Since fruit ripening can be spread over several weeks within the same bract depending on the time flowers were open for fertilization, covering allowed us to wait for all fruits to ripen without fruit being removed. Due to the large number of possible fruits produced by an entire inflorescence, we randomly selected two of the bracts on each inflorescence. Within these bracts we counted the number of mature fruits and the total number of flowers that were attempted, but whose ovules failed to develop. The pedicel of unsuccessful flowers can usually still be observed long after the flower has passed making an assessment of 'total flower attempts' possible. Because larger plants (i.e., those with more bracts or flowers) are likely to produce a higher absolute number of fruits than smaller plants, even if pollination rates are the same, we used the proportion of successful fruits out of the total number of fruits attempted on the two bracts as our response variable for fruit set (i.e., PropMature = mature fruits/total attempted fruits). This method was chosen to account for possible differences in plant vigor.

Seed set.- Each successful fruit can produce between one and three seeds. We collected all mature fruits from the two randomly selected bracts on our focal plants and counted the number of seeds contained in each fruit. Similar to the methods for proportion of successful fruits, we controlled for plant vigor by using the proportion of seeds produced out of what was possible given the number of successfully fertilized fruits (i.e., Proportion of seeds produced = total # seeds/total mature fruit*3). We chose the successful fruits in lieu of total fruits attempted since the reasons that fruit development

might be unsuccessful extend beyond pollination (e.g., fruits can fail due to insect damage, fungus, rotting, water availability, etc.). Constraining our examination to successful fruits tightens the inference for pollination per se. We also expect that this response variable is the one most likely to be reflective of differences in quality of pollen delivered, since it is the highest level of reproductive success we measured and plants have been shown to select against low quality pollen at multiple stages (Barrett 2002) including pollen germination (Kress 1983, Ramsey and Vaughton 2000), ovule fertilization and/or ovule development (Waser and Price 1991, Ramsey and Vaughton 2000).

4.2.10 Statistical models

We used linear mixed effects models (LMEs) to account for our study design which had multiple plants nested within each patch. Each patch was treated as a random effect and all other variables were treated as fixed effects. All models were fit using R 2.15.1 (R Core Team 2012) with the 'lme' routine (Bates 2012) using Gaussian family or 'lmer' using the binomial family (Bates et al. 2012) depending on the response variable (i.e., normally distributed errors versus dichotomous response variable). We visually assessed linear regression assumptions by examining linearity using x/y scatterplots of candidate variables and the assumption of normally distributed residuals using histograms of the residuals. When necessary, response variables were transformed to meet assumptions of normality. We used Akaike's information criterion (AIC) for model selection (Burnham and Anderson 2002).

To test our landscape change hypotheses we used a sequential modeling approach. We first selected the top local site variables. We did this by fitting pollination success models using each local site factor and ranking them using AIC. For models within two **Δ**AICc points of the top model we examined 90% confidence intervals. We considered a local site variable to be important when it had 90% confidence intervals that did not include zero. Secondly, we selected the top composition variables using the same approach. Once our top local and composition models were determined, we used AIC to assess the weight of evidence for each of our four landscape hypotheses. We constructed our models such that each successive model controlled for the previous step. For the local hypothesis we

used the model containing only important local site factors (e.g., Pollination ~ local). We then controlled for local site variability by including the top local factors in all models examining composition and configuration variables. For example, to test the landscape composition hypothesis we used the top composition and local variables (e.g., Pollination ~ local + composition). If no composition variables were found to be important in the above variable selection steps (i.e., **Δ**AICc of all composition models > null) then we used amount of forest within 1000 m since this was the *a priori* extent chosen for study design. We used forest patch size plus the top local factors to examine the landscape fragmentation hypothesis (e.g., Pollination ~ local + patch size). Despite the fact that our sampling was designed to separate the confounding of composition from configuration we also used a more conservative approach of controlling for composition statistically (e.g., Pollination ~ local + composition + patch size). We evaluated the fragmentation threshold hypothesis by examining the interaction between patch size and composition. (e.g., Pollination ~ patch size * composition + local). We did not have any variables that were highly correlated ($r > 0.7$) in the same model.

We chose to examine both years combined. We were expecting that landscape effects driven by composition and configuration would be similar from one year to the next as the landscape has remained relatively unchanged. However, the possibility exists for yearly differences driven by weather or other factors, so we tested for year effects by examining year interactions for all covariates that were found to be statistically important (i.e., 90% confidence intervals that do not include zero).

4.3 Results

We found pollen tubes in 64% of flowers we sampled. Pollen tubes were found in flowers from 36 of the 37 patches indicating that pollinators were present in all patches except one. When pollen tubes were detected within a flower we found an average of 2.4 tubes/style. Eighty-six percent of the plants produced at least one mature fruit and the average successful development rate for fruits was 18%. Within the successfully

pollinated fruits we found that on average only 45% of the total possible seeds were produced, given that each fruit can produce up to three seeds.

4.3.1 Local

Presence of pollen tubes.- The top local model for presence of pollen tubes was the total number of ornithophilous flowers within 20 m of the focal plant (**Δ**AICc to null = 0.55, Table 4.1a). The number of flowers had a weak positive effect, but had 90% confidence intervals that included zero (0.25±0.156; [-0.008, 0.514]), (estimate [β]±SE; [upper, lower 90% CI]). All other local scale variables had 90% confidence intervals that included zero.

Fruit success.- Since zero inflated- binomial models failed to converge for the fruit success response variable, we used a two step approach to account for the zero inflation. First we examined whether a plant produced at least one successful fruit. Secondly within the plants that had at least one successful fruit we looked at the proportion of fruits that were successful. For successful production of at least one fruit, total number of ornithophilous flowers was also the top local predictor (**Δ**AICc to null = 0.92, Table 4.1a). The number of flowers had a positive effect and had 90% confidence intervals that did not include zero (0.3±0.18; [0.009, 0.600]). We found little support for a change in the relationship of number of flowers to presence of fruit by year ('year*flowers' = 0.002±0.42). For proportion of successful fruits (within the plants that successfully produced at least one fruit) the top local models were plant height and number of bracts on the inflorescence (Table 4.1a). Both height (-0.25±0.087; [-0.39, -0.104], **Δ**AICc to null = 5.86) and bracts (-0.22±0.09; [-0.37, -0.074], **Δ**AICc to top model = 1.86) had negative effects on the proportion of successful fruits and confidence intervals that excluded zero. Neither response was affected by year ('height*year'= 0.13±0.19; [-0.25, 0.51], 'bracts*year'=0.007±0.2; [-0.4, 0.42]).

Seed set.- Species richness of ornithophilous plants within 20 m was the only local scale variable found to influence seed production (**Δ**AICc to null = 0.73, Table 4.1a). Increasing richness of ornithophilous plants showed a weak negative effect on the

proportion of possible seeds produced (-0.029 ±0.017; [-0.001, -0.058], Fig. 4.4). We found no support for the relationship between richness and seed changing with year ('year*richness'= -0.038±0.038, [-0.0993, 0.0242]).

4.3.2 Composition-'amount'

We found little support for effects of either amount of forest or amount of heliconia habitat on any of our response variables. For presence of pollen tubes, presence of fruit, proportion of fruit and proportion of possible seeds the 'null' model was the best-supported model (Table 4.1b). All forest and habitat amount variables had confidence intervals that included zero, regardless of scale.

4.3.3 Composition-'matrix'

Presence of pollen tubes.- The amount of resources in the matrix within 1000 m of the focal plant was the top model for matrix affects on presence of pollen tubes (**Δ**AICc to null = 0.7 ,Table 4.1c). Increasing resources in the matrix had a weak positive effect, but with confidence intervals that included zero (0.25±0.16, [-0.004, 0.519]).

Matrix resources did not affect the other three response variables. For presence of fruit, proportion of fruit and proportion of possible seeds the 'null' model was the best-supported model (Table 4.1c). Both scales of matrix counts had confidence intervals that included zero.

4.3.4 Configuration

Presence of pollen tubes.- We found little support for any effects of landscape configuration on the presence of pollen tubes (Table 4.2a). The 'null' model was the best supported and all effects had confidence intervals that included zero (Table 4.3a).

Fruit success.- Presence of successful fruit was best predicted by 'local' factors alone, but the second best supported model did include patch size (Table 4.2b). The top model for proportion of mature fruits was also the local variables on their own. However, the patch size plus local model was the second best once again (Table 4.2b). Model averaged estimates are shown (Table 4.3b, c).

Seed set.- The top model for proportion of possible seeds was the effect of patch size while controlling for local factors (**Δ**AICc to null = 4.7). Patch size was in the top three models. Patch size had a positive effect on the proportion of seeds produced (Table 4.3d, Fig. 4.5). The effect of patch size was still present after statistically controlling for amount of forest within the landscape (0.051±0.02; [0.018, 0.084]). The interaction of patch size and amount of forest model was the second most supported model (**Δ**AICc to top model = 1.3), but the interaction had confidence intervals that included zero (Table 4.3d). We found some evidence for a weakened patch size effect in the second year (-0.06±0.034; [-0.12, -0.008]).

4.3.5 Per hectare seed output

We examined the per hectare seed output to see if the proportional increase in seed success we found at the plant-level translated into differences in patch level output. This addressed the question of whether larger patches are producing more seeds per hectare than small patches. We calculated the seed per hectare output using the average density of heliconia within the patch (i.e., the average of all 20 m conspecific counts from the focal plants), the average number of bracts per heliconia and the average number of seeds per bract. We found little support for an effect of patch size on per hectare seed production (0.15±0.19; [-0.17, 0.47]). Rather, seeds per hectare were driven exclusively by elevation (0.54±0.18; [0.22, 0.86]). Elevation is also the most important driver of *H. tortuosa* densities (0.38±0.13; [0.17, 0.59]) suggesting that differences in plant per hectare plant densities in our sampled patches are currently large enough to compensate for any per capita differences in seed success rates.

4.3.6 Pollinator abundance

We captured Green Hermits (*Phaethornis guy*) in even the smallest (<2 ha) and most isolated (<8% forest within 1000 m) patches that we sampled. Green Hermit abundance did not appear to be affected by either patch size (0.42±0.5; [-0.47, 1.3], r^2=0.06, n=14) or proportion of forest (0.83±1.7; [-2.13, 3.45], r^2=0.02, n=14). However, when we looked at the abundance of *H. tortuosa* pollinators more generally we found that total

abundance was higher in larger patches (2.4±0.57; [1.42, 3.45], r^2=0.64, n=14, Fig. 4.6). This positive association of patch size with abundance of pollinators was still present after statistically controlling for the effect of proportion of forest within the landscape (psize = 9.23±3.06; [3.8, 14.8], pf1000 = -3.63±3; [-9.1, 1.9], r^2=0.65, n=14).

4.4 Discussion

Our results supported the landscape fragmentation hypothesis. The proportion of *H. tortuosa* seeds produced per plant increases with the size of tropical forest patches. This effect was independent of both local site conditions and the amount of forest in the landscape. This suggests that landscape configuration is important to *H. tortuosa* reproduction.

Relatively few studies have tested for independent configuration effects on pollination. We know of only one other study that examines an independent effect of patch size on seed set. Diekotter et al. (2007) used a manipulative experiment to examine the effect of patch size on seed set and pollinator visitation rates of red clover (*Trifolium pretense*), but found no significant differences due to patch size. Contrary to our results seed set and visitation rates in their system were driven primarily by habitat area and matrix type (Diekotter et al. 2007). If previous patch size studies are examined more broadly it is apparent that although they do not account for changes in landscape composition there are numerous studies documenting 'apparent' patch size effects on fruit or seed set (Wolf and Harrison 2001, Jacquemyn et al. 2002, Aguilar and Galetto 2004, Johnson et al. 2004, Kolb 2005, Valdivia et al. 2006, Yates et al. 2007, Matesanz et al. 2009). Though we cannot readily interpret how much of the variation is attributable to differences in patch size rather than changes in composition, these findings do suggest that patch size may be having important effects on pollination in other systems. Other studies have also documented little effect of changes in patch size (Ward and Johnson 2005, Slagle and Hendrix 2009) or have found even higher seed set in small patches (Goverde et al. 2002). However the relative contribution of patch size versus changes in composition is unclear.

We expect that the patch size effect that we found is a result of either changes in pollinator densities, pollinator movements or both. We found that the relative abundance of legitimate heliconia visitors increased with increasing forest patch size. This effect was independent of the total amount of forest in the landscape and therefore represents an independent effect of landscape configuration. Independent patch size effects have been documented in other pollinator taxa. For example, Steffan-Dewenter and Schiele (2008) statistically controlled for habitat amount and show that increasing patch size had a positive effect on bee abundance. Cresswell and Osborne (2004) also found a positive effect of increasing patch size on bee visitation rates using a manipulative experiment. Other studies have suggested that landscape transformation might be important for hummingbirds (Borgella et al. 2001), but were unable to attribute the effects to either composition or configuration. Hummingbirds were less abundant and visited flowers at a lower rate in small fragments than in contiguous forest in a study examining the combined effects of habitat loss and fragmentation (Valdivia et al. 2006). Similar to our results, the number of seeds per fruit was also lower in fragments than contiguous forest in this study (Valdivia et al. 2006). In contrast, work in Brazil showed that hummingbirds were relatively unaffected by landscape changes (Stouffer and Bierregaard 1995). However, it is important to point out that in this system the native habitat to matrix contrast is relatively low (forest/regenerating forest) compared to our system (forest/pasture or intensive agriculture). In some instances disturbance can increase flowering resources compared to intact forest (Linhart et al. 1987) and this is thought to have been likely in the Brazil study system (Stouffer and Bierregaard 1995). The regenerating forest surrounding forest patches in the Brazil study may even have had higher resources than the intact areas. It is also worth noting that the abundance of Green Hermits, the most frequent visitor of *H. tortuosa* within our study region, was unaffected by patch size. We captured Green Hermits in even the smallest and most isolated patches suggesting that all plants have access to these pollinators irrespective of landscape context. This ubiquitous availability of at least some level of pollinator visitation is also born out by the fact that pollen tubes were present on plants from all but one of our thirty-seven patches.

The movements of hummingbirds in this system also appear to be affected by landscape configuration. Experimental translocations revealed that Green Hermits, a relatively generalist species, avoided crossing non-forested areas when possible (Hadley and Betts 2009). When moving through agricultural landscapes they took much longer and more torturous paths in order to avoid the intervening agricultural matrix. This suggests that movements across gaps are likely less frequent than movements within forest, potentially resulting in higher rates of pollen flow over equivalent distances within forest compared to through the matrix. A recent study examining passive movements of hummingbirds in a temperate rainforest system documented significant differences in movement frequency depending on landscape type (Magrach et al. 2012). Hummingbirds crossed gaps quite readily if gaps were low contrast and contained trees, but the number of crossings decreased as interpatch distance increased in higher contrast open-matrix types (Magrach et al. 2012).

Landscape configuration effects on pollinator movements have been shown in a number of other systems. Townsend and Levey (2005) used a large scale landscape manipulation to show that corridors increase pollen movement between patches, suggesting that non-habitat gaps are representing barriers to pollen flow in their grassland system. Cranmer et al. (2012) found that linear landscape elements helped direct bee flight movements and this directional response had a profound effect on plant reproductive success. Plants had increased pollinator activity, pollen receipt and subsequent seed set in patches with more connections (Cranmer et al. 2012). Green Hermits are one of the more generalist traplining hummingbird species; it is not unrealistic to expect movements of other specialized pollinators (Borgella et al. 2001) of *H. tortuosa* may also be affected by landscape structure. It is also likely that our hummingbird capture data may provide an additional indication of higher movement rates to plants within large patches. It is possible that higher capture rates reflect higher rates of movement by birds coming to plants from longer distances away in large patches. The lower relative hummingbird abundance in small patches possibly reflects lower rates of hummingbird visitation to these sites. This means that not only may there be more pollinators in the larger patches they may be moving over longer distances.

Hummingbirds delivering more pollen, higher quality pollen, or both could drive the configuration effects on proportion of seed produced. However there are some indications that this may be largely a quality effect. When pollen tubes are present the average number is 2.43 tubes/style. Only 3 tubes/style are required in order to have complete seed set (Kress 1983) suggesting that flowers visited by hummingbirds are receiving ~80% of the quantity of pollen that is needed. However, the average number of seeds per fruit is much lower (~45% of possible within successful fruits) suggesting that even though a sufficient number of pollen grains germinated, not all of the ovules were fertilized. It is likely that since *H. tortuosa* can have pollen tubes produced from pollination visits delivering both self and outcross pollen, many of the pollen tubes are actually from self pollination events. Ovule fertilization and subsequent seed set may be more frequent with outcross pollen. The discrepancy between the relatively high percentage of flowers with pollen tubes (64%) versus the low proportion of fruit (18%) and seed set (45% of possible seeds within successful fruit) is potentially explained by plants receiving largely self-pollen or pollen from closely related individuals. It is likely that the patch size effects in this system are at least partially driven by differences in pollen quality. Small patches may be receiving little outcross pollen from beyond the boundaries of the patch and plants could be receiving mainly within-patch pollen because of restricted hummingbird movements. While in one *Heliconia* species it was documented that outbreeding depression may occur over relatively short distances (Schleuning et al. 2009), the importance of landscape scale factors to seed set suggest that this is unlikely to be the case in our system.

Increasing pollinator densities has been shown to increase pollination success for many different plant communities (Kearns et al. 1998, Knight et al. 2005) and pollinator density has also been shown to correlate with seed quantity (Plowright and Hartling 1981). However, successive benefits of increasing pollinator densities on plant reproduction are thought to attenuate as other factors such as pollen quality or plant vigor become more limiting (Geib and Galen 2012). If the differences in pollination found in our system were purely a function of pollinator abundance, as opposed to differences in movement patterns, we would expect that there would be fewer visits to plants in small patches and

therefore fewer flowers with pollen tubes. Yet, we found no effect of patch size on the presence of pollen tubes. Pollen tubes can be found after a single pollinator visit (unpublished data). The equal proportion of flowers visited on plants in patches of different sizes suggests that differences in seed set due to patch size are not simply a result of more pollinators in large patches, but also more pollen movement over longer distances. Similar to our finding, Farwig et al. (2009) used a mensurative experiment to show that isolation reduced seed set, but not visitation rates in a fly and bee pollinated system.

Contrary to what we expected based on general effects of landscape disturbance on biodiversity (Fahrig 2003), we found little support for an effect of landscape composition in this system. Amount of forest, amount of *H. tortuosa* habitat and matrix resource abundance all had little effect on the pollination response variables we examined. This is in contrast with several studies that have documented primarily effects of forest or habitat amount on pollination (Larsen et al. 2005, Diekotter et al. 2007, Garcia and Chacoff 2007, Taki et al. 2007) or pollinators (Holzschuh et al. 2010) in other systems. However, at very low levels of forest it becomes increasingly difficult to discriminate between effects of patch size and forest amount. Our conclusions regarding the lack of support for landscape composition effects should be interpreted cautiously. However, the lack of support for a composition effect in our system further suggests that the seed-set difference we are documenting may be largely due to gap crossing avoidance on the part of the pollinators and differing movement behavior depending on landscape configuration. Hummingbirds are highly vagile (Moore et al. 2008) and documented gap crossing avoidance (Hadley and Betts 2009, Magrach et al. 2012) is likely behavioral. Movements across open areas could be influenced by perceived risk of predation even if the probability of mortality is low (Lima 1991) or inadequate resource benefits to warrant repeated crossings (Hinsley 2000). Less frequent movements across open areas would result in most pollen movement happening only within a patch.

Resources available within the matrix appeared to have little effect on pollination in our system. We only observed a non-significant positive effect of the matrix resources within

the 1000 m extent on presence of pollen tubes, indicating that there might be more hummingbird visits in sites surrounded by resource-rich matrix. Matrix resources did not appear to have any influence on our other response variables. Matrix resources are hypothesized to have important effects on pollinator abundance and behavior in disturbed landscapes (Jules and Shahani 2003). In our system it is unclear to what extent the pollinators of *H. tortuosa* use resources within the matrix, but it appears that matrix resources have little effect on heliconia reproduction.

Local conditions do appear to be important for pollination of *H. tortuosa*. The random sample hypothesis was the best-supported model for all of our response variables other than seed-set. Characteristics of the local flowering community appeared to be particularly important. Presence of both pollen tubes and fruit was affected by the total number of ornithophilous flowers within 20 m of the focal plant. Plants with more ornithophilous flowers surrounding them tended to be more likely to have pollen tubes and to have fruit present. This suggests that a plant is more likely to be visited when located in a flower-rich site. Much of the work investigating the effect of floral neighborhood has focused on conspecific densities and has documented positive effects of increasing density on pollinator visitation rates (Bosch and Waser 2001, Jakobsson et al. 2009) or pollination success (Roll et al. 1997, Knight 2003, Kirchner et al. 2005). Knight (2003) showed experimentally that plant reproductive success increases asymptotically with increasing floral density in a temperate herb. Feinsinger et al. (1991) showed that increasing either con or heterospecifc densities of two tropical species increased the rate at which hummingbirds visited focal plants.

We found a negative effect of local flower richness on proportion of seeds produced. This supports the interspecific flower competition hypothesis that suggests that co-flowering species may affect the quality of pollination services provided by pollinators (Levin and Anderson 1970). Other studies have shown empirical support for negative effects of the presence of heterspecific flowers on seed set. In extreme cases, such as those involving alien flower species, heterospecific flowers have been shown to disrupt pollination systems (Aizen et al. 2008, Carvalheiro et al. 2008). Seed set in the mixed flower patches

has been shown to be reduced by 25% relative to pure patches (Chittka and Schurkens 2001). Jakobsson et al. (2009) also showed that the amount of compatible pollen delivered depended on the number of heterspecifics in the area for a self-incompatable herb. However, not all studies examining floral neighborhood have documented negative effects (Aizen 1997, Somanathan et al. 2004). The fact that heterospecific competition has been documented in two different hummingbird pollination systems is of particular relevance to our findings. Caruso (1999) used experimental density manipulations of two temperate hummingbird pollinated plants to show that conspecific pollen deposition on *Ipomopsis aggregate* was reduced when *Castilleja linariaefolia* was present and the number seeds set per fruit was reduced by up to 17%. Similarly, Feinsinger and Tiebout (1991) use a laboratory experiment on a tropical hummingbird system to show that intervening visits to heterospecifc flowers strongly reduced pollen transfer among conspecific flowers. In a second field study they showed that increasing either conspecific or heterospecific densities increased visitation rates by hummingbirds, but that in the presence of heterospecifcs, pollen transfer was much lower (Feinsinger et al. 1991). Hummingbirds in our system may be delivering lower quality pollen loads (e.g., mixed pollen loads, less *H. tortuosa* pollen, higher proportion of self pollen) in sites with a greater richness of heterspecific flowers if similar effects exist.

Plant size appeared to affect the proportion of fruits that were successful. Both plant height and inflorescence size had negative effects on the proportion of successful fruits. This could be due to plant vigor if larger plants are only able to produce a smaller proportion of the fruits they attempt. It could also be that hummingbirds visit a smaller proportion of the open flowers within a large inflorescence or conversely, they may apply more self-pollen by visiting many flowers on one plant successively (Plowright and Hartling 1981). Pollinator visitation rates have been shown to be proportionately lower in situations of high floral offering (Garcia-Robledo et al. 2005) and competition for visits within individual inflorescences can limit the percent fruit set (Menges 1995).

We attempted to control for the potential confounding influences of plant vigor (Knight et al. 2005) by including proportional fruit and seed set measures as opposed to absolute

fruit and seed production. However, we cannot fully exclude the possibility that our differences in seed set could represent differences in plant vigor for plants in small versus large patches. If this were the case we would expect to find patch size affects on plant size. However, we found no effect of patch size on either of our plant size measures (height = 0.035±0.09; [-0.11, 0.11], number of bracts = 0.036±0.08; [-0.53, 0.17]). Furthermore, plant size did not appear to be a good predictor of proportion of seeds produced. Both plant height and number of bracts had a negative effect on the proportion of fruits that were successful, suggesting that when effects of vigor are present they can be accounted for by these plant size metrics. We conducted a pollen supplementation experiment across our landscape, but supplemental hand pollinations proved unreliable in this species. Hand pollinations with self-pollen, local pollen from within 20 m and pollen from plants > 100 m away were all far less successful that open pollinated flowers. Unfortunately, the low success of hand pollinations prevented us from being able to test for differences in pollen quality and quantity limitation using this method.

We found some support for the landscape fragmentation hypothesis suggesting that habitat fragmentation might have a non-linear effect on heliconia pollination. The interaction model for composition and configuration was the second most supported model for seed set. This suggests that the effect of patch size may change depending on amount of forest within the landscape.

It is important to note that the effect of patch size on proportion of seeds was much weaker in the second year of our study. We found little difference in the average number of fruit or seeds per plant within our landscape between the two years suggesting that it is unlikely there were any dramatic environmental changes. However, our sample of patches was reduced in the second year (only 25 versus 34 patches). Unfortunately, this was further complicated by an apparent non-random exclusion of patches in the extremes of the patch size and forest amount gradient; more very large and very small patches were lost. This increased the confounding of patch size and habitat amount likely reducing out ability to detect effects.

Local *H. tortuosa* densities were unaffected by either patch size or amount of forest in the landscape, but were primarily driven by elevation. Plants were found at higher densities with increasing elevation irrespective of landscape scale factors. There are at least two possible hypotheses for the lack of any patch size effect on plant density despite apparent differences in seed success. First, seed dispersal could be unaffected by landscape structure resulting in continued recruitment in small patches. Alternatively many of the plants may be relics from pre-disturbance populations. *H. tortuosa* is able to reproduce vegetatively and clones are able to persist for long periods. The lack of a landscape configuration effect on plant densities could therefore be a sign of extinction debt in this system (Kuussaari et al. 2009).

Summary

Our work provides evidence for and effect of habitat fragmentation on *H. tortuosa* seed set, but not other aspects of plant reproduction such as pollen tube growth or fruit set. Increasing log-patch size had a positive effect on proportion of seeds produced independent of forest amount. Combined with the lack of support for landscape composition models, this suggests that configuration of the remaining forest may be more important to heliconia reproduction than the amount of forest in the landscape. We found that the relative abundance of pollinators was also configuration dependent. Patch size had a positive effect on the abundance of legitimate *H. tortuosa* pollinators independent of amount of forest in the landscape. In addition, movement patterns of even generalist pollinators in this system are limited by non-forested areas. We hypothesize that differences in pollen quality resulting from these changes in hummingbird movements and/or relative abundance are driving the configuration effects on heliconia reproduction we observe. In support of the random sample hypothesis, local floral conditions appear to be playing an important role in several aspects of pollination. Presence of pollen tubes and successful fruits were best explained by local flower densities implying that plants surrounded by more flowers appear to be more likely to receive hummingbird visits. However, local ornithophilous flower richness had a negative effect on proportional seed set suggesting interspecific competition from co-flowering species could be reducing the quality of pollen delivered. Long-term conservation of this species may be best

accomplished by maintaining large patches of tropical forest, particularly at high elevation where plant densities are greatest. Increasing connectedness of forest patches may also facilitate movement of pollinators and subsequently pollen flow among patches.

TABLE 4.1. Comparison of local site and landscape composition models for the presence of pollen tubes, presence of mature fruit, proportion of mature fruit and proportion of possible seeds produced by *H. tortuosa*. The number of parameters (K), Akaike's Information Criterion (AICc), weights (w_i), and evidence ratios (ER) based on the top ranked model are shown. Best-supported models are shown in bold.

(a) Local

	Presence of pollen tubes					Presence of mature fruit					Proportion mature fruit					Proportion of possible seeds				
Model	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER
null	2	282.37	0.55	0.20	1.32	2	231.92	0.92	0.17	1.58	3	877.75	5.86	0.03	18.70	3	-15.00	0.73	0.16	1.44
height	3	284.30	2.48	0.07	3.45	3	233.45	2.44	0.08	3.39	**4**	**871.89**	**0.00**	**0.63**	**1.00**	4	-14.55	1.19	0.13	1.81
bracts	NA	NA	NA	NA	NA	3	233.96	2.96	0.06	4.39	**4**	**873.75**	**1.86**	**0.25**	**2.53**	4	-13.54	2.19	0.08	2.97
edge	3	284.42	2.59	0.07	3.66	3	233.79	2.79	0.07	4.04	4	879.05	7.16	0.02	35.88	4	-14.56	1.17	0.13	1.80
stream	3	283.14	1.32	0.13	1.93	3	232.49	1.49	0.13	2.11	4	879.68	7.79	0.01	49.13	4	-13.05	2.69	0.06	3.87
elevation	3	283.76	1.94	0.10	2.64	3	233.96	2.96	0.06	4.40	4	879.63	7.74	0.01	47.90	4	-13.39	2.35	0.07	3.22
heto	3	284.14	2.32	0.08	3.19	3	233.93	2.93	0.06	4.32	4	879.51	7.62	0.01	45.23	4	-12.93	2.80	0.06	4.06
flowers	**3**	**281.82**	**0.00**	**0.26**	**1.00**	**3**	**231.00**	**0.00**	**0.27**	**1.00**	4	879.80	7.90	0.01	52.05	4	-13.69	2.05	0.08	2.80
richness	3	284.07	2.25	0.08	3.08	3	232.70	1.70	0.11	2.34	4	879.73	7.84	0.01	50.35	**4**	**-15.73**	**0.00**	**0.23**	**1.00**
global	9	290.84	9.02	0.00	90.84	10	241.09	10.09	0.00	155.01	11	882.85	10.96	0.00	240.14	11	-4.20	11.54	0.00	320.63

(b) Composition - 'amount'

	Presence of pollen tubes					Presence of mature fruit					Proportion mature fruit					Proportion of possible seeds				
Model	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER
null	**2**	**282.37**	**0.00**	**0.17**	**1.00**	**2**	**231.92**	**0.00**	**0.30**	**1.00**	**3**	**877.75**	**0.00**	**0.28**	**1.00**	**3**	**-15.00**	**0.00**	**0.25**	**1.00**
pf500	3	283.76	1.38	0.09	2.00	3	233.54	1.62	0.13	2.25	4	879.31	1.57	0.13	2.19	4	-14.97	0.03	0.25	1.01
pf1000	3	282.81	0.44	0.14	1.25	3	233.79	1.86	0.12	2.54	4	878.99	1.24	0.15	1.86	4	-13.37	1.63	0.11	2.26
pf2000	3	282.47	0.10	0.16	1.05	3	233.82	1.90	0.12	2.58	4	879.77	2.02	0.10	2.75	4	-12.94	2.06	0.09	2.80
ht500	3	282.42	0.05	0.17	1.02	3	233.96	2.04	0.11	2.77	4	879.81	2.07	0.10	2.81	4	-13.01	1.99	0.09	2.70
ht1000	3	282.44	0.06	0.17	1.03	3	233.82	1.90	0.12	2.58	4	879.77	2.02	0.10	2.74	4	-12.93	2.06	0.09	2.81
ht2000	3	283.27	0.89	0.11	1.56	3	233.96	2.04	0.11	2.77	4	878.96	1.21	0.15	1.83	4	-13.45	1.55	0.12	2.17

(c) Composition- 'matrix'

	Presence of pollen tubes					Presence of mature fruit					Proportion mature fruit					Proportion of possible seeds				
Model	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER	K	AICc	ΔAICc	wi	ER
null	2	282.37	0.70	0.31	1.42	**2.00**	**231.92**	**0.00**	**0.37**	**1.00**	**3.00**	**877.75**	**0.00**	**0.58**	**1.00**	**3.00**	**-15.00**	**0.00**	**0.46**	**1.00**
mtrx500	3	282.92	1.25	0.24	1.87	3.00	232.64	0.72	0.26	1.43	4.00	879.80	2.05	0.21	2.79	4.00	-13.88	1.12	0.26	1.75
mtrx1000	**3**	**281.67**	**0.00**	**0.45**	**1.00**	3.00	231.93	0.01	0.37	1.01	4.00	879.81	2.06	0.21	2.80	4.00	-13.96	1.04	0.27	1.68

Notes: Local variables are - height (plant height), bracts (number of bracts on the inflorescence), edge (distance to the nearest edge), stream (distance to the nearest stream), elevation (elevation at the plant), heto (number of flowering *H. tortuosa* plants within 20m), flowers (total number of ornithophilous flowers), richness (ornithophilous flower richness), global (all local variables). Composition 'amount' variables are - pf500 (proportion of forest within 500 m), pf1000 (proportion of forest within 1000 m), pf2000 (proportion of forest within 2000 m), ht500 (amount of heliconia habitat within 500 m), ht1000 (amount of heliconia habitat within 1000 m), ht2000 (amount of heliconia habitat within 2000 m). Composition 'matrix' variables are - mtrx500 (ornithophilous flowers in matrix within 500 m), mtrx1000 (ornithophilous flowers in matrix within 1000 m)

TABLE 4.2. Comparison of landscape change hypotheses models and heliconia habitat amount models for the presence of pollen tubes, presence of mature fruit, proportion of mature fruit and proportion of possible seeds produced by *H. tortuosa*. The number of parameters (K), Akaike's Information Criterion (AICc), weights (w_i), and evidence ratios (ER) based on the top ranked model are shown. The number of parameters (K), Akaike's Information Criterion (AICc), weights (w_i), and evidence ratios (ER) based on the top ranked model are shown.

Model	**K**	**AICc**	**ΔAICc**	**w_i**	**ER**
(a) Presence of pollen tubes					
flowers	3	281.82	0.00	0.31	1.00
null	2	282.37	0.55	0.23	1.35
pf1000+flowers	3	282.81	0.75	0.22	1.41
psize+flowers	3	284.42	2.05	0.11	2.82
psize+pf1000+flowers	4	284.62	2.72	0.08	3.86
psize*pf1000+flowers	5	284.87	3.51	0.05	6.20
(b) Presence of mature fruit					
flowers	3	231.00	0.00	0.29	1.00
psize+flowers	4	231.16	0.16	0.27	1.08
null	2	231.92	0.92	0.18	1.58
pf1000+flowers	4	232.79	1.79	0.12	2.44
psize+pf1000+flowers	5	233.23	2.23	0.10	3.05
psize*pf1000+flowers	6	234.96	3.96	0.04	7.25
(c) Proportion mature fruit					
height+bracts	5	871.83	0.00	0.38	1.00
psize+height+bracts	6	872.32	0.49	0.30	1.28
pf1000+height+bracts	6	873.45	1.62	0.17	2.24
psize+pf1000+height+bracts	7	874.41	2.58	0.10	3.63
psize*pf1000+height+bracts	8	876.54	4.71	0.04	10.54
Null	3	877.75	5.92	0.02	19.27
(d) Proportion possible seeds					
psize+richness	5	-19.71	0.00	0.46	1.00
psize*pf1000+richness	7	-18.40	1.30	0.24	1.92
psize+pf1000+richness	6	-17.76	1.95	0.17	2.65
richness	4	-15.73	3.97	0.06	7.29
null	3	-15.00	4.71	0.04	10.52
pf1000+richness	5	-13.97	5.74	0.03	17.62

Notes: flowers (total number of ornithophilous flowers), pf1000 (proportion of forest within 1000 m), psize (log forest patch size), height (plant height), bracts (number of bracts on the inflorescence), richness (ornithophilous flower richness).

TABLE 4.3. Model averaged estimates effects on the presence of pollen tubes, presence of mature fruit, proportion of mature fruit and proportion of possible seeds produced by *H. tortuosa*. The model average estimates, standard errors (SE), number of models containing each variable (N_{models}), upper (U90% CI) and lower (L90% CI) 90% confidence intervals and relative variable importance are shown. Variables with 90% confidence intervals excluding zero are shown in bold.

Variable	Estimate	SE	N_{models}	L90% CI	U90% CI	RVI
(a) Presence of pollen tubes						
flowers	0.240	0.156	4	-0.017	0.497	0.77
pf1000	-0.181	0.160	3	-0.444	0.082	0.35
psize	-0.004	0.168	3	-0.281	0.273	0.24
psize*pf1000	0.206	0.183	1	-0.095	0.507	0.05
(b) Presence of mature fruit						
flowers	**0.305**	**0.180**	**4**	**0.009**	**0.600**	0.82
psize	0.252	0.191	3	-0.063	0.566	0.41
pf1000	0.061	0.200	3	-0.269	0.390	0.26
psize*pf1000	0.126	0.211	1	-0.221	0.473	0.04
(c) Proportion mature fruit						
height	**-0.193**	**0.095**	**4**	**-0.350**	**-0.036**	0.98
bracts	-0.140	0.099	4	-0.303	0.024	0.98
psize	0.128	0.106	3	-0.052	0.307	0.42
pf1000	0.050	0.115	3	-0.140	0.241	0.31
psize*pf1000	0.004	0.115	1	-0.186	0.194	0.04
(d) Proportion possible seeds						
psize	**0.045**	**0.020**	**3**	**0.012**	**0.079**	0.87
richness	**-0.030**	**0.016**	**4**	**-0.057**	**-0.003**	0.96
psize*pf1000	**0.033**	**0.020**	**1**	**0.001**	**0.066**	0.24
pf1000	-0.002	0.020	3	-0.035	0.031	0.44

Notes: flowers (total number of ornithophilous flowers), pf1000 (proportion of forest within 1000 m), psize (log forest patch size), height (plant height), bracts (number of bracts on the inflorescence), richness (ornithophilous flower richness).

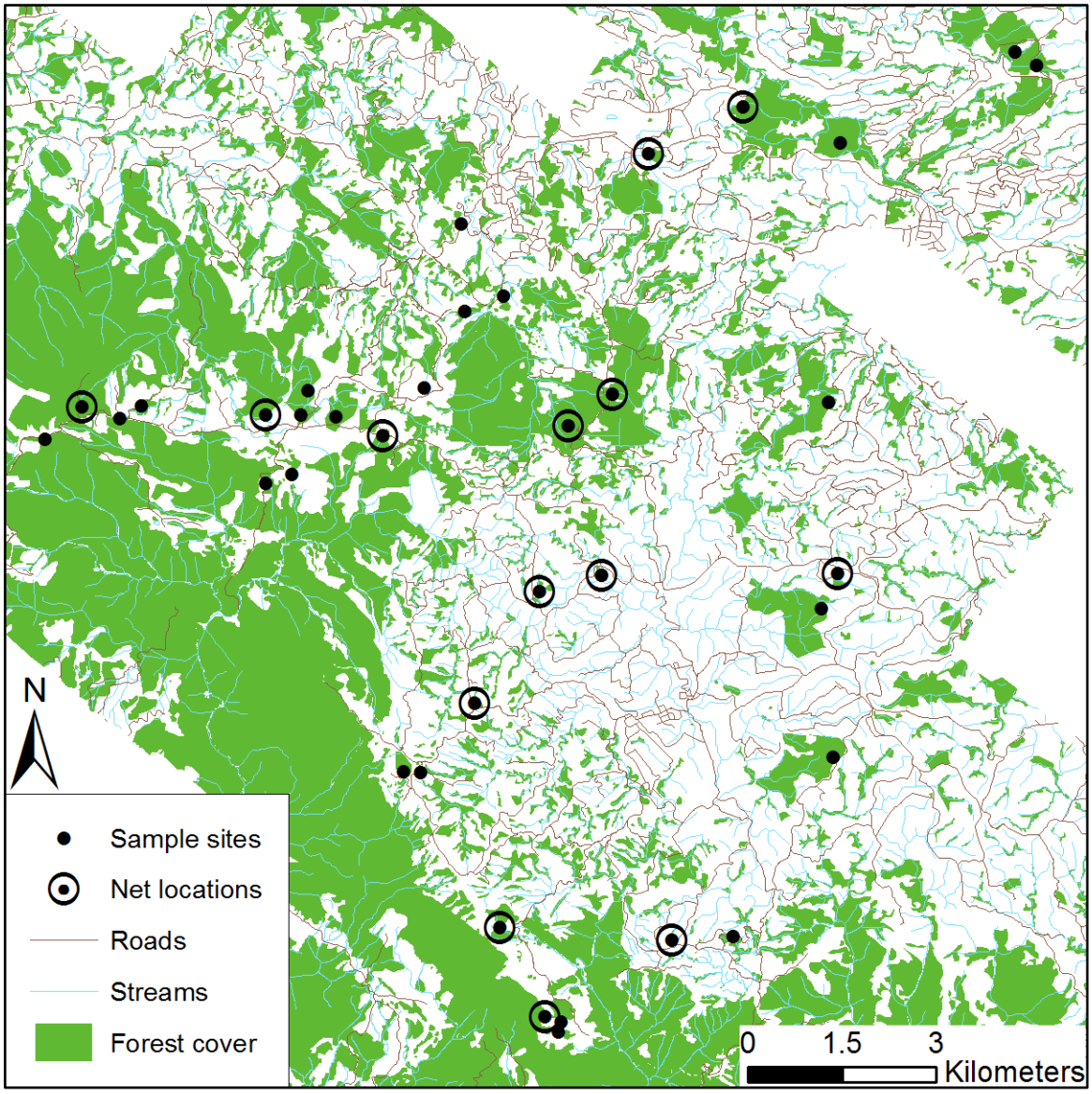

FIGURE 4.1. Map of the study area in Coto Brus, Costa Rica showing the plant and hummingbird sampling locations.

FIGURE 4.2. Inflorescence of a *Heliconia tortuosa* showing red bracts and yellow flowers. A developing fruit can be seen at the base of the lower bract. Photo credit: Matt Betts

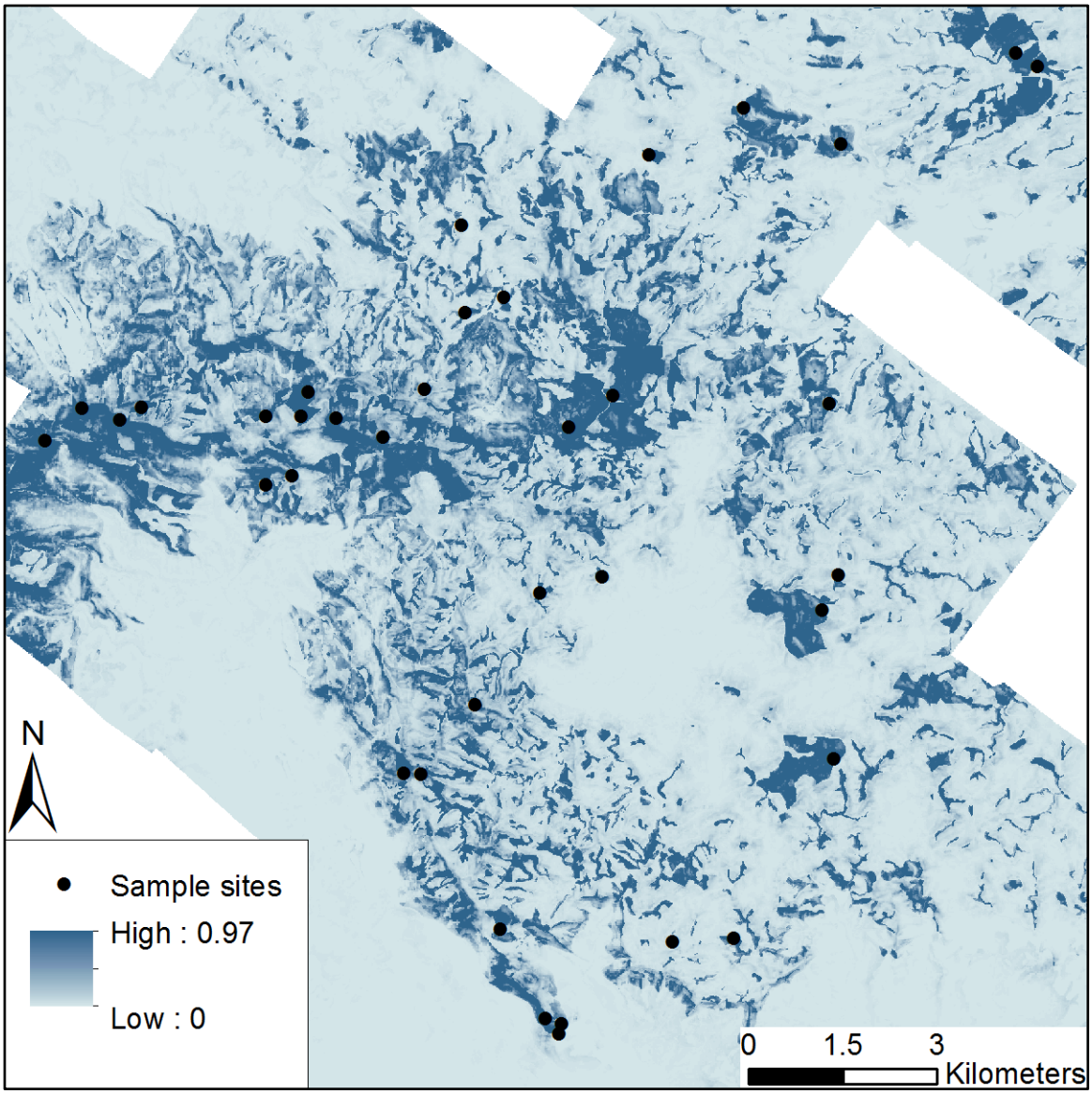

FIGURE 4.3. Map of *H. tortuosa* habitat suitability generated from location data using maximum entropy modeling software (MaxEnt). Darker shades indicate higher suitability.

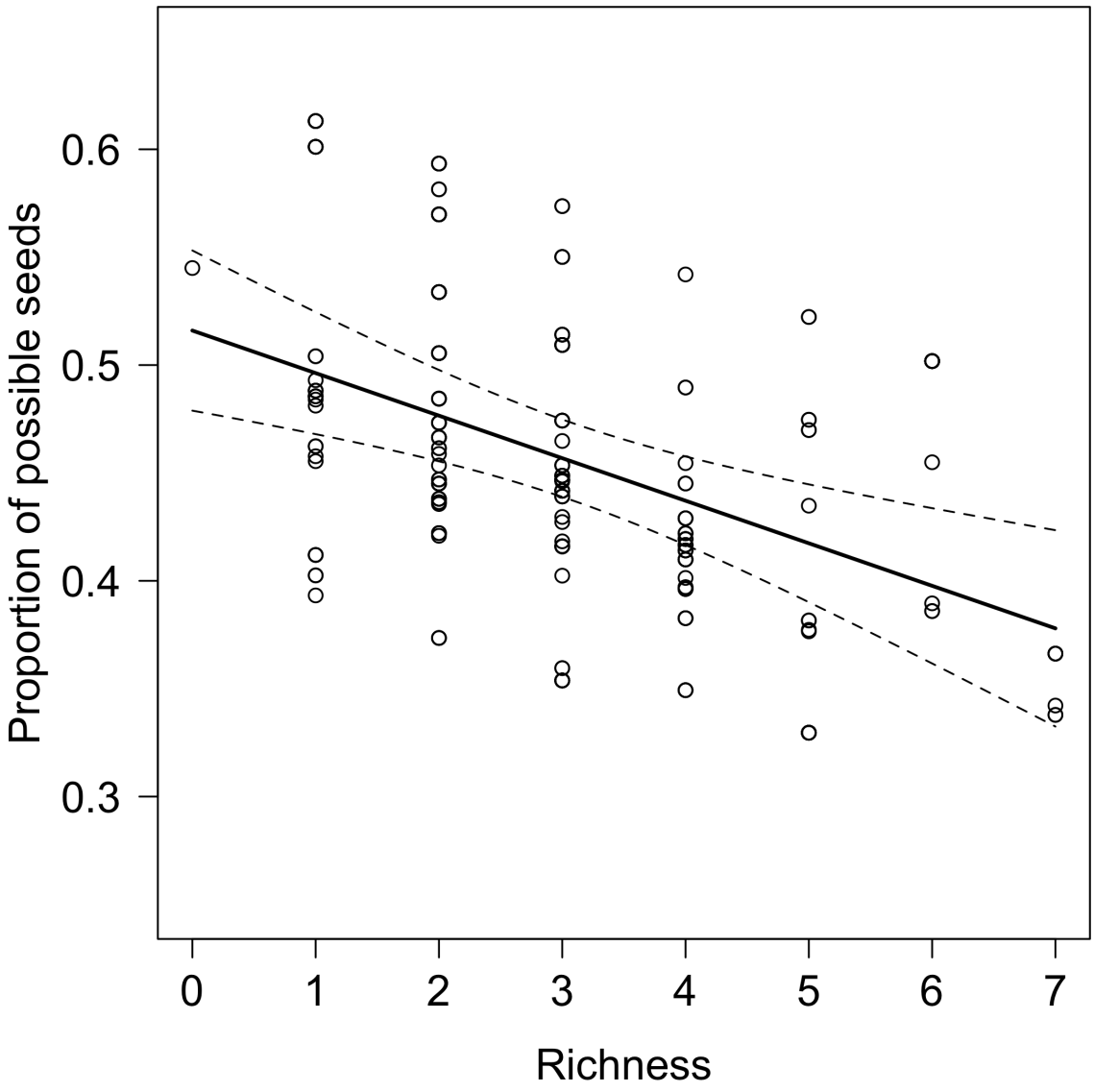

FIGURE 4.4. Increasing richness of ornithophilous flowers at the local site scale has a negative effect on proportion of possible seeds produced. The solid line indicates the modeled relationship between proportion of possible seeds and richness. The dotted line represents the standard error of that relationship. The open circles are the fitted values from the model: proportion of possible seeds ~ log patch size + ornithophilous flower richness.

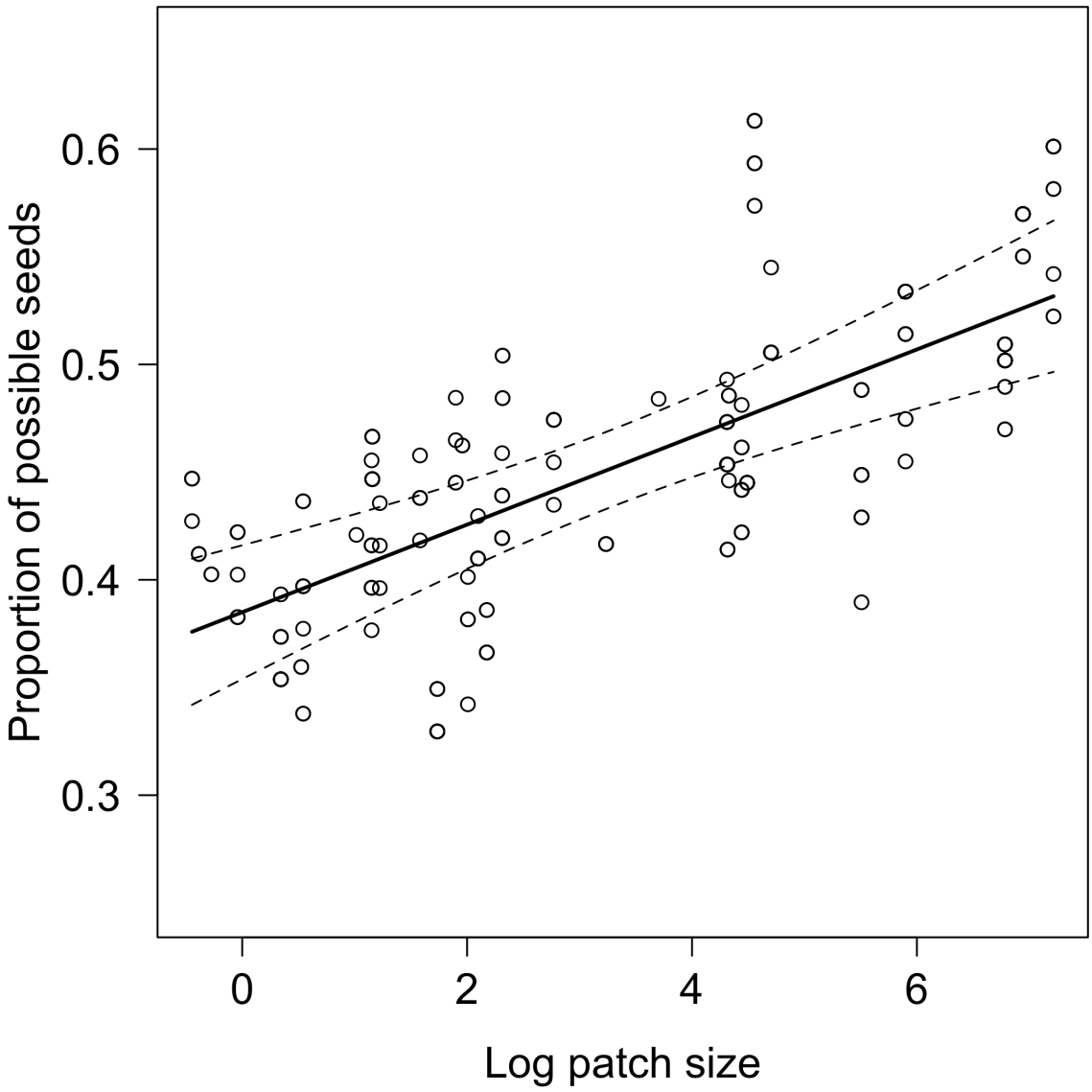

FIGURE 4.5. Proportion of possible seeds produced increases with increasing log forest patch size. The solid line indicates the modeled relationship between proportion of possible seeds and log patch size. The dotted line represents the standard error of that relationship. The open circles are the fitted values from the model: proportion of possible seeds ~ log patch size + ornithophilous flower richness.

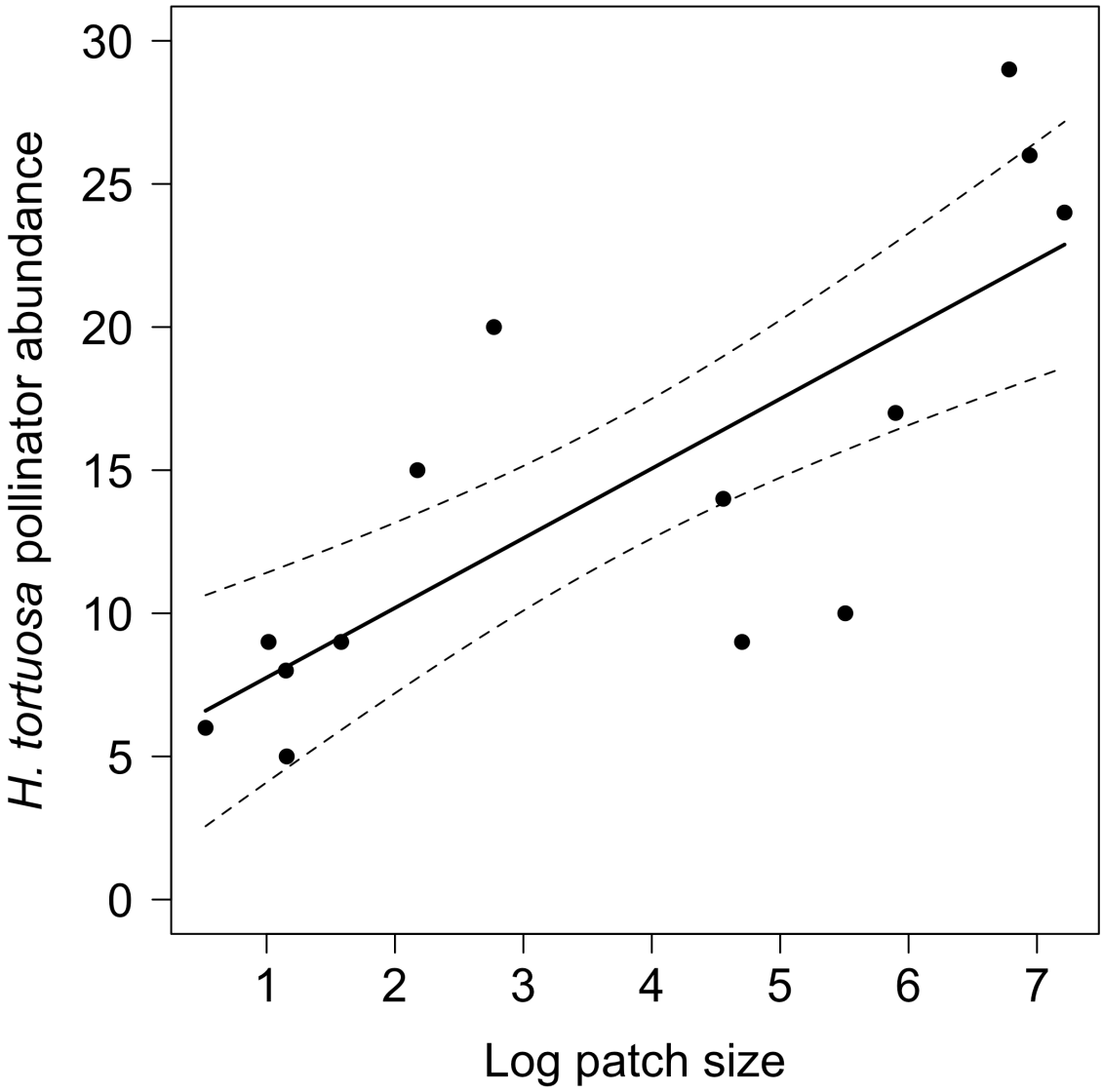

FIGURE 4.6. Abundance of legitimate *H. tortuosa* pollinators increased with increasing log forest patch size. The solid line indicates the modeled relationship between hummingbird abundance and log patch size. The dotted line represents the standard error of that relationship. The filled circles are the data points.

5 CONCLUSION

My dissertation research investigates the effects of landscape change on pollination. I used a combination of literature review, experiments and descriptive fieldwork to investigate how independent effects of changes in landscape composition or configuration could affect pollination. I was able to gain deeper insight into landscape dependent pollination declines by merging ideas from the fields of pollination ecology, landscape ecology and behavioral ecology.

In my second chapter I examined how landscape disturbance primarily influences three components of pollination interactions: pollinator density, pollinator movement, and plant demography. I argue that effects of habitat loss on each of these components are likely to differ substantially from the effects of fragmentation, which is likely to be more complex and may influence each pollination component in contrasting ways. However, despite the potential for independent effects of habitat fragmentation on pollination I found very few studies designed to test for these effects. I reviewed existing work and found only six of 303 studies considering the influence of landscape context on pollination separated the effects of habitat loss from fragmentation. Therefore, almost no research exists on whether landscape composition (i.e. the relative abundance of land cover types, particularly the amount of habitat) or landscape fragmentation (e.g. corridors, patch size and shape), or both, are most critical to pollination dynamics.

Given the high degree of uncertainty about the relative importance of fragmentation effects in pollination declines, I argue that is it particularly important to consider configuration in future landscape pollination studies. Without understanding the drivers of pollination and pollinator declines it will be impossible to conceptualize optimal landscape designs for maintaining or enhancing pollination services (Kremen et al. 2007).

I expect that variation across studies in findings regarding the effects of ‘fragmentation’ on pollination results from artifacts of sampling designs. In particular, studies were typically ineffective at separating fragmentation from habitat loss and had mismatches in spatial scale between the landscapes studied and the ecological processes of interest. I

suggest that researchers should adopt an organism-based view of the landscape and measure elements of interest accordingly (Betts et al. 2006).

I provide three main recommendations for future studies. First, studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines, implementing effective conservation measures, and optimizing ecosystem services in complex landscapes. Secondly, I recommend a combination of experimental and observational studies, designed to better understand the movement capacities and behavioral decisions of pollinators. Thirdly, further progress in this field will require consistency in terminology and clearly defined methodologies.

In my third chapter used experimental translocations coupled with novel radio-tagging technology to investigate movements of Green Hermit hummingbirds under different landscape contexts. I show that even a generalist species with high vagility avoids crossing open matrix in favor of longer forested detours. These changes in movement patterns as a function of landscape context could have profound impacts on pollen flow and the persistence of many plant species. My work adds to a growing body of evidence for the importance of remnant forest strips and riparian buffers (i.e., corridors) in highly modified landscapes (Cranmer et al. 2012). Maintenance of forest along hedgerows or streams will likely facilitate inter-patch movements and should be important for pollen transfer events. I predict that fidelity to linear forest habitats by hummingbird pollinators could 'scale up' to result in fragmentation effects on plant demography that are independent of the detrimental influence of habitat loss.

In my fourth chapter I examine a plant species *H. tortuosa* that depends on hermit and hermit-like hummingbirds for pollination services (Stiles and Freeman 1993) to see if differences in hummingbird movements do in fact scale up to affect plant reproduction in this system. I used a mensurative experiment designed to allow me to tease apart the effects of landscape configuration from those of composition. I found evidence for an effect of habitat fragmentation on *H. tortuosa* seed set, but not other aspects of plant reproduction such as pollen tube growth or fruit set. Increasing log-patch size had a

positive effect on proportion of seeds produced independent of forest amount. Combined with the lack of support for the landscape composition hypothesis, this suggests that configuration of the remaining forest may be more important to heliconia reproduction than the amount of forest in the landscape. Therefore, from a conservation perspective not all forest is equal and it is likely that large patches are of higher value for maintaining effective pollination.

I also examined relative abundance of hummingbirds across patches of different size to test if the pollinator density hypothesis could be explaining these patch size effects. I found that the relative abundance of pollinators was also configuration dependent with patch size having a positive effect on the abundance of pollinators independent of amount of forest in the landscape. Unfortunately, it is not currently possible for me to attribute the differences in seed set to differences in relative pollinator densities versus patterns of their movement (Chapter 3). However, I hypothesize that differences in pollen quality resulting from changes in hummingbird movements and/or relative abundance are driving the configuration effects on heliconia reproduction I observe.

In support of the random sample hypothesis, local floral conditions appear to be playing an important role in several aspects of pollination. Presence of pollen tubes and successful fruits were best explained by local flower densities, implying that plants surrounded by more flowers appear to be more likely to receive hummingbird visits. However, local ornithophilous flower richness had a negative effect on proportional seed set suggesting interspecific competition from co-flowering species could be reducing the quality of pollen delivered. I suggest that long-term conservation of this species may be best accomplished by maintaining large patches of tropical forest, particularly at high elevation where plant densities are greatest. Increasing connectedness of forest patches may also facilitate movement of pollinators and subsequently pollen flow among patches.

This work should be accompanied with a few important caveats which I discuss here: My use of experimental translocations to measure functional connectivity was necessary in order to standardize motivation (Bélisle 2005). This allowed me to examine how the hummingbirds responded to different landscape elements when trying to return to their

home range. However, by translocating the birds I placed them in experimental situations where their behavior may differ from passive movements. Work comparing daily movement patterns to movement data from my translocation experiments will be an important next step in determining how reflective these homing experiments are at reflecting daily foraging decisions. Further efforts can also be well spent towards creating maps of landscape resistance using data from the translocation experiments. Using these resistance values, functional connectivity could be calculated for different locations within the landscape. These connectivity measures could then be used as additional configuration metrics to examine whether plant reproduction can be explained using these measures of functional isolation. Detailed habitat use data from tagged hummingbirds could also be used to generate species-centered habitat suitability maps. This should enable the generation of more biologically relevant measures of habitat patch size and amount for pollinators.

Unfortunately, the failure of my pollen supplementation experiment weakened my ability to control for plant vigor and test for the relative importance of pollen quantity versus quality. I was forced to use indexes of heliconia vigor (Bruna and Kress 2002) such as plant height and inflorescence size as secondary measures. Resolving the issues associated with hand supplementation of this species would open a number of possibilities to tighten the inference of my fourth chapter. Using a series of pollen supplementation treatments (control, self-pollen, local pollen, among patch pollen and open pollinated flowers) it would be possible to not only control for plant vigor, but also to test a series of hypotheses to determine the relative contribution of quantity and quality limitation across the landscape gradient. It would also enable effects to be assigned to differences in visitation, local pollen flow or longer distance pollen dispersal.

Currently we can only speculate what the long-term population effects of differing seed production rates in small patches might be. Use of vegetation surveys to sample the demographic structure of heliconia across the landscape gradient would be quite informative. If the current lack of a patch size effect on flowering heliconia *density* is a sign of extinction debt in this system, then I would expect to see fewer seedlings in small

patches. Examining additional factors such as seed germination rates would be helpful to determine if seeds from larger patches were also those most likely to germinate successfully. If the higher proportion of seeds produced in large patches reflects higher rates of outcross pollen it is quite possible that germination rates might be higher (Yang and Hodges 2010). In addition, this system provides an excellent opportunity to test for independent composition and configuration effects on landscape genetics. Detailed knowledge of pollinator movements and adequate study designs have been woefully lacking in most landscape pollination genetics work (Chapter 2). If higher seed set in large patches is due to improved outcrossing rates from increased hummingbird movements then, I would expect seeds from plants in large patches to show higher rates of heterozigosity. If seed set differences are simply a function of higher visitation rates, then I would expect little genetic difference.

In future work, it will be important to test how translocations reflect daily hummingbird movements. This passive and experimental movement data can serve an additional purpose as the basis to generate maps of hummingbird habitat and functional connectivity. These pollinator-centered landscape views may provide additional insight into heliconia pollination declines. Continued experiments to refine hand-supplementation techniques could reveal important information on the mechanics behind successful hummingbird pollination and allow for more rigorous controlled pollination experiments across the landscape. Germination trials, demographic testing and landscape genetics are all obvious next steps.

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APPENDICES

APPENDIX A. Details of the 303 articles examined in Chapter 2. FT = Fragmentation in title, Discuss = Indicates whether an article discusses their results as being the effects of habitat fragmentation, Separate = Indicates if a study separates composition from configuration, Y = Yes, N = No, NA = Not applicable.

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Adriaens	2009	Acta Oecologica-International Journal of Ecology	Conservation of remnant populations of Colchicum autumnale - The relative importance of local habitat quality and habitat fragmentation	Y	patch size, isolation	seed set	Y	N	none	N
Andrieu	2009	Acta Oecologica-International Journal of Ecology	The town Crepis and the country Crepis: How does fragmentation affect a plant-pollinator interaction?	N	isolation	visitation rates	Y	N	none	N
Ashworth	2009	Biological Conservation	Pollinator-dependent food production in Mexico	N			NA	NA	NA	Y
Bezerra	2009	Journal of Animal Ecology	Pollination networks of oil-flowers: a tiny world within the smallest of all worlds	N			N	N	none	N
Brosi	2009	Biological Conservation	The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini)	Y	isolation, patch size, edge	pollinator abundance/diversity	Y	N	none	N
Bruna	2009	Journal of Vegetation Science	Habitat fragmentation and plant populations: is what we know demographically irrelevant?	Y			NA	NA	NA	Y
Campagne	2009	Population Ecology	Fine-scale response to landscape structure in Primula vulgaris Huds.: does hedgerow network connectedness ensure connectivity through gene flow?	N	corridors	pollen movement	Y	N	none	N
Cottrell	2009	Heredity	Contemporary pollen flow, characterization of the maternal ecological neighbourhood and mating patterns in wild cherry (Prunus avium L.)	N	disturbed/ undisturbed	pollen movement	Y	N	none	N
De-Lucas	2009	Molecular Ecology	Spatial genetic structure in continuous and fragmented populations of Pinus pinaster Aiton	N	disturbed/ undisturbed	genetic diversity	Y	N	none	N
Dunley	2009	Biotropica	Reproduction of Byrsonima sericea (Malpighiaceae) in Restinga Fragmented Habitats in Southeastern Brazil	N	patch size, isolation	seed set, visitation rates	Y	N	none	N
Dutra	2009	Plant Species Biology	Reproductive biology of Cyrtopodium punctatum in situ: implications for conservation of an endangered Florida orchid	N	habitat quality	pollination, visitation rates	Y	N	none	N
Farwig	2009	Landscape Ecology	Isolation from forest reduces pollination, seed predation and insect scavenging in Swiss farmland	N	habitat loss, isolation	seed set, visitation rates	Y	Y	mensurative experiment	N
Fatemi	2009	Biological Conservation	Life on the edge - High levels of genetic diversity in a cliff population of Bertya ingramii are attributed to B-rosmarinifolia (Euphorbiaceae)	N	isolation	genetic diversity	Y	N	none	N
Gonzalez-Varo	2009	Biological Conservation	Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (Myrtus communis)	Y	patch size, isolation	seed set, visitation rates	Y	N	none	N
Hadley	2009	Biology Letters	Tropical deforestation alters hummingbird movement patterns	N	disturbed/ undisturbed	pollinator movement	Y	N	none	N
Hannon	2009	Biological Conservation	Hedgerows in an agri-natural landscape: Potential habitat value for native bees	N	habitat quality	pollinator abundance/diversity	N	N	none	N
Hinners	2009	American Midland Naturalist	Receptiveness of Foraging Wild Bees to Exotic Landscape Elements	N	patch size	pollinator diet shift	Y	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Huang	2009	Biological Conservation	Impact of proximity to a pathway on orchid pollination success in Huanglong National Park, South-West China	N	edge	pollination	N	N	none	N
Jauker	2009	Landscape Ecology	Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat	N	isolation, matrix quality	pollinator abundance/diversity	N	N	none	N
Johnson	2009	Biology Letters	Relationships between population size and pollen fates in a moth-pollinated orchid	N	isolation	pollination, seed set	N	N	none	N
Keitt	2009	Ecological Applications	Habitat conversion, extinction thresholds, and pollination services in agroecosystems	N	habitat loss, isolation	pollination, pollinator abundance/diversity, pollinator diet shift	Y	Y	simulation	Y
Krauss	2009	Journal of Applied Ecology	Habitat area but not habitat age determines wild bee richness in limestone quarries	N	patch size, edge	pollinator abundance/diversity	Y	N	none	N
Krauss	2009	Heredity	Contrasting impacts of pollen and seed dispersal on spatial genetic structure in the bird-pollinated Banksia hookeriana	N	isolation	pollen movement	N	N	none	N
Kuldna	2009	Ecological Economics	An application of DPSIR framework to identify issues of pollinator loss	N			NA	NA	NA	Y
Lander	2009	Revista Chilena De Historia Natural	Flower and fruit production and insect pollination of the endangered Chilean tree, Gomortega keule in native forest, exotic pine plantation and agricultural environments	N	disturbed/ undisturbed	seed set	Y	N	none	N
Levin	2009	Journal of Ecology	Enhancement of Allee effects in plants due to self-incompatibility alleles	N	patch size	pollination	N	N	none	N
Lewis	2009	Basic and Applied Ecology	Biodiversity change and ecosystem function in tropical forests	N			NA	NA	NA	Y
Liu	2009	Oecologia	Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive Solanum	N	habitat quality	pollination	N	N	none	N
Lopes	2009	Biological Conservation	Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments	N	patch size	pollination	Y	N	none	N
Matesanz	2009	Ecology	Impact of three global change drivers on a Mediterranean shrub	N	patch size	seed set	Y	N	none	N
McPhee	2009	Northeastern Naturalist	Past and Present Distribution of New Brunswick Bur Oak Populations: A Case for Conservation	N	isolation	genetic diversity	Y	N	none	N
Mehes	2009	Journal of Plant Ecology-Uk	Assessing genetic diversity and structure of fragmented populations of eastern white pine (Pinus strobus) and western white pine (P-monticola) for conservation management	N	patch size, isolation	genetic diversity	Y	N	none	N
Meyer	2009	Basic and Applied Ecology	Contrasting resource-dependent responses of hoverfly richness and density to landscape structure	N	habitat loss	pollinator abundance/diversity	Y	N	none	N
Mimura	2009	Molecular Ecology	Comparison of contemporary mating patterns in continuous and fragmented Eucalyptus globulus native forests	N	disturbed/ undisturbed	pollen movement, genetic diversity	Y	N	none	N
Ottewell	2009	Biological Conservation	Predicting reproductive success of insect- versus bird-pollinated scattered trees in agricultural landscapes	N	isolation	seed set	Y	N	none	N
Perez-Barrales	2009	Journal of Biogeography	Geographic variation of flower traits in Narcissus papyraceus (Amaryllidaceae): do pollinators matter?	N	isolation	genetic diversity	N	N	none	N
Pisanu	2009	Biotropica	Reproduction in Wild Populations of the Threatened Tree Macadamia tetraphylla: Interpopulation Pollen Enriches Fecundity in a Declining Species	N	patch size	pollination	Y	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Prober	2009	Agriculture Ecosystems & Environment	Enhancing biodiversity persistence in intensively used agricultural landscapes: A synthesis of 30 years of research in the Western Australian wheatbelt	N			NA	NA	NA	Y
Rabasa	2009	Plant Ecology	Temporal variation in the effects of habitat fragmentation on reproduction of the Mediterranean shrub Colutea hispanica	Y	patch size, isolation	seed set	Y	N	none	N
Schleuning	2009	Basic and Applied Ecology	Negative effects of habitat degradation and fragmentation on the declining grassland plant Trifolium montanum	Y	patch size, isolation	seed set	Y	N	none	N
Schmucki	2009	Oecologia	Pollination and reproduction of a self-incompatible forest herb in hedgerow corridors and forest patches	N	patch size, isolation	pollination, seed set	Y	N	none	N
Schoville	2009	Molecular Ecology	Alpine biogeography of Parnassian butterflies during Quaternary climate cycles in North America	N	habitat loss	pollinator movement	N	N	none	N
Seltmann	2009	Basic and Applied Ecology	Mating system, outcrossing distance effects and pollen availability in the wind-pollinated treeline species Polylepis australis BITT. (Rosaceae)	N	isolation	seed set	Y	N	none	N
Seltmann	2009	Plant Ecology	Biparental inbreeding depression, genetic relatedness and progeny vigour in a wind-pollinated treeline species in Argentina	N	isolation	genetic diversity	Y	N	none	N
Slagle	2009	Oecologia	Reproduction of Amorpha canescens (Fabaceae) and diversity of its bee community in a fragmented landscape	N	patch size	seed set, pollinator abundance/diversity	Y	N	none	N
Sober	2009	Basic and Applied Ecology	Contrasting effects of plant population size on florivory and pollination	N	patch size	visitation rates	N	N	none	N
Thiel-Egenter	2009	Global Ecology and Biogeography	Effects of species traits on the genetic diversity of high-mountain plants: a multi-species study across the Alps and the Carpathians	N			NA	NA	NA	Y
Tsaliki	2009	Acta Oecologica-International Journal of Ecology	Fitness and survival in fragmented populations of Narthecium ossifragum at the species' range margin	N	patch size	seed set	Y	N	none	N
Vergara	2009	Agriculture Ecosystems & Environment	Pollinator diversity increases fruit production in Mexican coffee plantations: The importance of rustic management systems	N	habitat loss	pollinator abundance/diversity	N	N	none	N
Wilson	2009	Plant Ecology	Seed production in a threatened Aloe is not affected by bird exclusion or population size	N	patch size	pollination	Y	N	none	N
Winfree	2009	Ecology	A meta-analysis of bees' responses to anthropogenic disturbance	N			NA	NA	NA	Y
Agren	2008	Journal of Ecology	Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size	N	habitat quality	seed set	N	N	none	N
Aguirre	2008	Biological Conservation	Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest	Y	patch size	pollinator abundance/diversity	Y	N	none	N
Aizawa	2008	Journal of Biogeography	Imprint of post-glacial history in a narrowly distributed endemic spruce, Picea alcoquiana, in central Japan observed in nuclear microsatellites and organelle DNA markers	N	isolation	genetic diversity	N	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Bacles	2008	Heredity	Paternity analysis of pollen-mediated gene flow for Fraxinus excelsior L. in a chronically fragmented landscape	N	isolation	pollen movement	Y	N	none	N
Beatty	2008	Diversity and Distributions	Range-edge effects promote clonal growth in peripheral populations of the one-sided wintergreen Orthilia secunda	N	isolation	genetic diversity	Y	N	none	N
Born	2008	Molecular Ecology	Small-scale spatial genetic structure in the Central African rainforest tree species Aucoumea klaineana: a stepwise approach to infer the impact of limited gene dispersal, population history and habitat fragmentation	Y	isolation	genetic diversity	Y	N	none	N
Brosi	2008	Journal of Applied Ecology	The effects of forest fragmentation on bee communities in tropical countryside	Y	habitat loss, patch size, isolation	pollinator abundance/diversity	Y	N	none	N
de Lacerda	2008	Biotropica	Long-pollen movement and deviation of random mating in a low-density continuous population of a tropical tree Hymenaea courbaril in the Brazilian Amazon	N	isolation	pollen movement	N	N	none	N
Field	2008	Journal of Ecology	Relative frequency of sympatric species influences rates of interspecific hybridization, seed production and seedling performance in the uncommon Eucalyptus aggregata	N	patch size	seed set	Y	N	none	N
Hanson	2008	Molecular Ecology	Pollen dispersal and genetic structure of the tropical tree Dipteryx panamensis in a fragmented Costa Rican landscape	N	patch size, isolation	pollen movement, genetic diversity	Y	N	none	N
Hill	2008	Acta Oecologica-International Journal of Ecology	Mating strategies and pollen limitation in a globally threatened perennial Polemonium vanbruntiae	N	patch size	pollination	Y	N	none	N
Jones	2008	Proceedings of the Royal Society B-Biological Sciences	Neighbourhood density and genetic relatedness interact to determine fruit set and abortion rates in a continuous tropical tree population	N	isolation	pollination	Y	N	none	N
Kaneko	2008	Plant Species Biology	Genetic differentiation among populations of an oceanic island: The case of Metrosideros boninensis, an endangered endemic tree species in the Bonin Islands	N	isolation	genetic diversity	Y	N	none	N
Kelly	2008	New Zealand Journal of Ecology	Flower predation by Zelleria maculata (Lepidoptera) on Peraxilla mistletoes: effects of latitude and fragmentation, and impact on fruit set	Y	edge	seed set	Y	N	none	N
Kennedy	2008	Oecologia	The reproductive assurance benefit of selfing: importance of flower size and population size	N	patch size	pollination	Y	N	none	N
Kobayashi	2008	Ecological Research	Effects of habitat fragmentation on the three-way interaction among ants, aphids and larvae of the giant purple emperor, Sasakia charonda (Hewitson), a near-threatened butterfly	Y	habitat loss	pollinator abundance/diversity	Y	N	none	N
Kolb	2008	Biological Conservation	Habitat fragmentation reduces plant fitness by disturbing pollination and modifying response to herbivory	Y	patch size, isolation	visitation rates, seed set	Y	N	none	N
Kramer	2008	Conservation Biology	The paradox of forest fragmentation genetics	Y			NA	NA	NA	Y
Kwaiser	2008	Agriculture Ecosystems & Environment	Diversity and abundance of bees (Hymenoptera : Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes	N	habitat loss	pollinator abundance/diversity	N	N	none	N
Laurance	2008	Biological Conservation	Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory	Y			NA	NA	NA	Y

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Lopez-A	2008	Biotropica	Genetic structure in remnant populations of an endangered Andean Magnolia	N	isolation	genetic diversity	Y	N	none	N
Michaels	2008	Oecologia	Effects of population size on performance and inbreeding depression in Lupinus perennis	N	patch size	genetic diversity	Y	N	none	N
Oddou-Muratorio	2008	Molecular Ecology	Comparing direct vs. indirect estimates of gene flow within a population of a scattered tree species	N	isolation	genetic diversity	Y	N	none	N
Peterson	2008	Plant Ecology	Effects of population size on genetic diversity, fitness and pollinator community composition in fragmented populations of Anthericum liliago L	N	patch size	visitation rates	Y	N	none	N
Ricketts	2008	Ecology Letters	Landscape effects on crop pollination services: are there general patterns?	N	isolation	visitation rates, seed set	NA	NA	NA	Y
Rundlof	2008	Biological Conservation	Interacting effects of farming practice and landscape context on bumblebees	N	habitat loss	pollinator abundance/diversity	N	N	none	N
Sampson	2008	Molecular Ecology	Outcrossing between an agroforestry plantation and remnant native populations of Eucalyptus loxophleba	N	isolation	genetic diversity	Y	N	none	N
Sjodin	2008	Journal of Applied Ecology	The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects	N	habitat quality	visitation rates	N	N	none	N
Spigler	2008	Journal of Ecology	Effects of plant abundance on reproductive success in the biennial Sabatia angularis (Gentianaceae): spatial scale matters	N	isolation	pollination	N	N	none	N
Steffan-Dewenter	2008	Ecology	Do resources or natural enemies drive bee population dynamics in fragmented habitats?	N	habitat loss, patch size	pollinator abundance/diversity	Y	Y	statistical	N
Steffan-Dewenter	2008	Journal of Applied Ecology	The interplay of pollinator diversity, pollination services and landscape change	N			NA	NA	NA	Y
Tamaki	2008	Heredity	Genetic variation and differentiation in populations of a threatened tree, Magnolia stellata: factors influencing the level of within-population genetic variation	N	isolation	genetic diversity	N	N	none	N
Tscharntke	2008	Ecology	Landscape constraints on functional diversity of birds and insects in tropical agroecosystems	N			NA	NA	NA	Y
Winfree	2008	Journal of Applied Ecology	Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA	N	habitat loss	visitation rates	N	N	none	N
Albrecht	2007	Journal of Applied Ecology	The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland	N	habitat loss, isolation	pollination, visitation rates	Y	N	none	N
Arroyo-Rodriguez	2007	Biological Conservation	Impact of rain forest fragmentation on the population size of a structurally important palm species: Astrocaryum mexicanum at Los Tuxtlas, Mexico	Y			NA	NA	NA	Y
Bossuyt	2007	Conservation Biology	Genetic rescue in an isolated metapopulation of a naturally fragmented plant species, Pamassia palustris	N	patch size	genetic diversity	Y	N	none	N
Byrne	2007	Molecular Ecology	Extensive pollen dispersal in a bird-pollinated shrub, Calothamnus quadrifidus, in a fragmented landscape	N	patch size, isolation	pollen movement	Y	N	none	N
Diekotter	2007	Oikos	Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects	N	habitat loss, patch size, matrix quality	seed set, visitation rates	Y	Y	manipulative experiment	N
Garcia	2007	Conservation Biology	Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation	Y	habitat loss	pollination, seed set, visitation rates	Y	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Goldman	2007	Ecological Economics	Institutional incentives for managing the landscape: Inducing cooperation for the production of ecosystem services	N			NA	NA	NA	Y
Hirayama	2007	Biological Conservation	Reduced seed production, inbreeding, and pollen shortage in a small population of a threatened tree, Magnolia stellata	N	patch size	seed set	Y	N	none	N
Honnay	2007	Conservation Biology	Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation	Y	patch size	genetic diversity	Y	N	none	N
Isagi	2007	Ecological Research	Genetic and reproductive consequences of forest fragmentation for populations of Magnolia obovata	Y	disturbed/ undisturbed	seed set, genetic diversity	Y	N	none	N
Kremen	2007	Ecology Letters	Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change	N			NA	NA	NA	Y
Lopes	2007	Oecologia	Variation in pollinator assemblages in a fragmented landscape and its effects on reproductive stages of a self-incompatible treelet, Psychotria suterella (Rubiaceae)	N	habitat loss, isolation	pollinator abundance/diversity, pollination, seed set	Y	N	none	N
Mathiasen	2007	Conservation Biology	Genetic structure and early effects of inbreeding in fragmented temperate forests of a self-incompatible tree, Embothrium coccineum	N	patch size, isolation	genetic diversity	Y	N	none	N
Merrett	2007	New Zealand Journal of Botany	Pollination performance and vulnerability to pollination breakdown of sixteen native shrub species from New Zealand	N	patch size	pollination, seed set	N	N	none	N
Ockinger	2007	Journal of Applied Ecology	Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes	N	isolation	pollinator abundance/diversity	Y	N	none	N
Oster	2007	Ecoscience	Sex ratio mediated pollen limitation in the dioecious herb Antennaria dioica	N	isolation	pollination	Y	N	none	N
Pauw	2007	Ecology	Collapse of a pollination web in small conservation areas	N	patch size	seed set, pollinator abundance/diversity	Y	N	none	N
Priess	2007	Ecological Applications	Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems	N	isolation	pollinator abundance/diversity, seed set	Y	N	none	N
Taki	2007	Landscape Ecology	Landscape effects of forest loss in a pollination system	N	habitat loss, edge	pollination, pollinator abundance/diversity	Y	N	none	N
Taki	2007	Biodiversity and Conservation	Does habitat loss affect the communities of plants and insects equally in plant-pollinator interactions? Preliminary findings	N	habitat loss	pollinator diet shift	N	N	none	N
Wagenius	2007	American Naturalist	Patch aging and the S-allee effect: Breeding system effects on the demographic response of plants to habitat fragmentation	Y	patch size	pollination	Y	N	none	N
Williams	2007	Ecological Applications	Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape	N	habitat quality	pollination	Y	N	none	N
Williams	2007	Biological Conservation	Genetic diversity and spatial structure of a keystone species in fragmented pine rockland habitat	N	patch size	pollination	Y	N	none	N
Willig	2007	Biotropica	Phyllostomid bats of lowland Amazonia: Effects of habitat alteration on abundance	N	disturbed/ undisturbed	pollinator abundance/diversity	Y	N	none	N
Winfree	2007	Conservation Biology	Effect of human disturbance on bee communities in a forested ecosystem	N	habitat loss	pollinator abundance/diversity	Y	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Yates	2007	Biological Conservation	Seed production, germinability and seedling growth for a bird-pollinated shrub in fragments of kwongan in south-west Australia	N	patch size	seed set	Y	N	none	N
Yates	2007	Biodiversity and Conservation	Composition of the pollinator community, pollination and the mating system for a shrub in fragments of species rich kwongan in south-west Western Australia	N	patch size	pollinator abundance/diversity, visitation rates	Y	N	none	N
Aguilar	2006	Ecology Letters	Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis	Y			NA	NA	NA	Y
Artz	2006	Journal of Ecology	The effects of neighbouring tree islands on pollinator density and diversity, and on pollination of a wet prairie species, Asclepias lanceolata (Apocynaceae)	N	patch size, isolation	pollination, pollinator abundance/diversity	N	N	none	N
Becker	2006	Biological Conservation	Effects of pollination distance on reproduction and offspring performance in Hypochoeris radicata: Experiments with plants from three European regions	N	isolation	genetic diversity	Y	N	none	N
Broadhurst	2006	Biological Conservation	Reproductive constraints for the long-term persistence of fragmented Acacia dealbata (Mimosaceae) populations in southeast Australia	N	patch size	seed set	Y	N	none	N
Burgess	2006	New Zealand Journal of Ecology	Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of Peraxilla tetrapetala (Loranthaceae)	N			NA	NA	NA	Y
Cane	2006	Ecological Applications	Complex responses within a desert bee guild (Hymenoptera : Apiformes) to urban habitat fragmentation	Y	patch size	pollinator abundance/diversity	Y	N	none	N
Chacoff	2006	Journal of Applied Ecology	Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest	N	isolation	pollinator abundance/diversity	Y	N	none	N
Degen	2006	Biological Conservation	Impact of selective logging on genetic composition and demographic structure of four tropical tree species	N	disturbed/ undisturbed	genetic diversity	N	N	none	N
Delaval	2006	Revue D Ecologie-La Terre Et La Vie	Edge effects on frugivorous and nectarivorous bat communities in a neotropical primary forest in French Guiana	N	edge	pollinator abundance/diversity	N	N	none	N
Diekotter	2006	Biodiversity and Conservation	Effects of landscape elements on the distribution of the rare bumblebee species Bombus muscorum in an agricultural landscape	N	habitat loss	pollinator abundance/diversity	N	N	none	N
Dupont	2006	Biological Conservation	Species composition, feeding specificity and larval trophic level of flower-visiting insects in fragmented versus continuous heathlands in Denmark	N	disturbed/ undisturbed	pollinator abundance/diversity	Y	N	none	N
Gonzales	2006	Molecular Ecology	Pollen-mediated gene dispersal within continuous and fragmented populations of a forest understorey species, Trillium cuneatum	N	disturbed/ undisturbed	pollen movement	Y	N	none	N
Herrerias-Diego	2006	Conservation Biology	Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree Ceiba aesculifolia	Y	habitat loss	seed set	Y	N	none	N
Klein	2006	Journal of Animal Ecology	Rain forest promotes trophic interactions and diversity of trap-nesting hymenoptera in adjacent agroforestry	N	isolation, edge	pollinator abundance/diversity	Y	N	none	N
Kolb	2006	Plant Ecology	Forest fragmentation and plant reproductive success: a case study in four perennial herbs	Y	patch size, isolation	visitation rates	Y	N	none	N
McFrederick	2006	Biological Conservation	Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera : Apidae)?	N	patch size, edge, matrix quality	pollinator abundance/diversity	N	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Mix	2006	Basic and Applied Ecology	Inbreeding and soil conditions affect dispersal and components of performance of two plant species in fragmented landscapes	N	patch size	pollination	Y	N	none	N
Olschewski	2006	Ecology and Society	Economic evaluation of pollination services comparing coffee landscapes in Ecuador and Indonesia	N	habitat loss	pollination, seed set	N	N	none	N
Ramos	2006	Biotropica	Floral visitors and pollination of Psychotria tenuinervis (Rubiaceae): Distance from the anthropogenic and natural edges of an Atlantic forest fragment	N	edge, isolation	seed set, visitation rates, pollinator abundance/diversity	Y	N	none	N
Segal	2006	Israel Journal of Ecology & Evolution	Fragmentation and pollination crisis in the self-incompatible Iris bismarckiana (Iridaceae), with implications for conservation	Y	habitat quality	pollination, seed set	Y	N	none	N
Sork	2006	Landscape Ecology	Genetic analysis of landscape connectivity in tree populations	N			NA	NA	NA	Y
Tomimatsu	2006	Population Ecology	Evaluating the consequences of habitat fragmentation: a case study in the common forest herb Trillium camschatcense	Y	patch size	seed set	Y	N	none	N
Valdivia	2006	Biodiversity and Conservation	Depressed pollination of Lapageria rosea Ruiz et pav. (Philesiaceae) in the fragmented temperate rainforest of Southern South America	N	patch size	pollination	Y	N	none	N
Van Rossum	2006	Perspectives in Plant Ecology Evolution and Systematics	Within-population genetic variation in the distylous Primula veris: Does floral morph anisoplethy matter in fragmented habitats?	N	habitat quality	genetic diversity	Y	N	none	N
Van Rossum	2006	Acta Oecologica-International Journal of Ecology	Morph-specific differences in reproductive success in the distylous Primula veris in a context of habitat fragmentation	Y	patch size	seed set	Y	N	none	N
Wagenius	2006	Ecology	Scale dependence of reproductive failure in fragmented Echinacea populations	N	patch size, isolation	pollination, seed set	Y	N	none	N
Bacles	2005	Evolution	Historical and contemporary mating patterns in remnant populations of the forest tree Fraxinus excelsior L	N	patch size	genetic diversity	Y	N	none	N
Cairns	2005	Biotropica	Bee populations, forest disturbance, and africanization in Mexico	N	disturbed/ undisturbed	pollinator abundance/diversity	N	N	none	N
de Jong	2005	Acta Oecologica-International Journal of Ecology	Distance-dependent pollen limitation of seed set in some insect-pollinated dioecious plants	N	isolation	pollination	Y	N	none	N
Garcia-Robledo	2005	Biotropica	Equal and opposite effects of floral offer and spatial distribution on fruit production and predispersal seed predation in Xanthosoma daguense (Araceae)	N	isolation	seed set	N	N	none	N
Ghazoul	2005	Trends in Ecology & Evolution	Buzziness as usual? Questioning the global pollination crisis	N			NA	NA	NA	Y
Honnay	2005	New Phytologist	Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species	Y			NA	NA	NA	Y
Kolb	2005	Journal of Ecology	Reduced reproductive success and offspring survival in fragmented populations of the forest herb Phyteuma spicatum	N	patch size, isolation	pollination	Y	N	none	N
Kolb	2005	Conservation Biology	Effects of life-history traits on responses of plant species to forest fragmentation	Y	patch size, isolation	pollination syndrome	Y	N	none	N
Kremen	2005	Frontiers in Ecology and the Environment	A call to ecologists: measuring, analyzing, and managing ecosystem services	N			NA	NA	NA	Y

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Larsen	2005	Ecology Letters	Extinction order and altered community structure rapidly disrupt ecosystem functioning	N	habitat loss	pollination	Y	N	none	N
Mayfield	2005	Ecology	Species and functional diversity of native and human-dominated plant communities	N	disturbed/ undisturbed	pollination syndrome	N	N	none	N
Parachnowitsch	2005	Canadian Field-Naturalist	Insect visitation to wildflowers in the endangered Garry Oak, Quercus garryana, ecosystem of British Columbia	N	habitat quality	visitation rates	N	N	none	N
Pearson	2005	Biological Conservation	Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change	Y			NA	NA	NA	Y
Townsend	2005	Ecology	An experimental test of whether habitat corridors affect pollen transfer	N	corridors	pollination, pollen movement, pollinator movement	N	Y	manipulative experiment	N
Tscharntke	2005	Ecology Letters	Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management	N			N	N	NA	Y
Ward	2005	Oikos	Pollen limitation and demographic structure in small fragmented populations of Brunsvigia radulosa (Amaryllidaceae)	N	patch size, isolation	pollination	N	N	none	N
Yates	2005	Conservation Biology	Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape	N	disturbed/ undisturbed	pollination	Y	N	none	N
Aguilar	2004	Oecologia	Effects of forest fragmentation on male and female reproductive success in Cestrum parqui (Solanaceae)	Y	patch size	pollination	Y	N	none	N
Amarasekare	2004	Journal of Animal Ecology	Spatial dynamics of mutualistic interactions	N			NA	NA	NA	Y
Ashworth	2004	Journal of Ecology	Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation?	Y			NA	NA	NA	Y
Bach	2004	New Zealand Journal of Ecology	Effects of forest edges, fruit display size, and fruit colour on bird seed dispersal in a New Zealand mistletoe, Alepis flavida	N	edge	seed set	Y	N	none	N
Bacles	2004	Molecular Ecology	Genetic effects of chronic habitat fragmentation on tree species: the case of Sorbus aucuparia in a deforested Scottish landscape	Y	disturbed/ undisturbed	genetic diversity	Y	N	none	N
Brys	2004	Journal of Ecology	Reduced reproductive success in small populations of the self-incompatible Primula vulgaris	N	patch size	seed set	Y	N	none	N
Chacoff	2004	Biotropica	Effects of fragmentation on amount of aborted and predated seed in the Chaco Serrano Argentina	Y	patch size	seed set	Y	N	none	N
Cresswell	2004	Journal of Applied Ecology	The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow	N	habitat loss, patch size, isolation	visitation rates, genetic diversity	Y	Y	manipulative experiment	N
De Marco	2004	Biodiversity and Conservation	Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production	N	isolation	pollination	Y	N	none	N
Duncan	2004	Journal of Ecology	Plant isolation reduces outcross pollen receipt in a partially self-compatible herb	N	isolation	pollen movement	Y	N	none	N
Ghazoul	2004	Biotropica	Alien abduction: Disruption of native plant-pollinator interactions by invasive species	N	habitat quality	pollinator movement, pollinator diet shift	Y	N	none	N
Ghazoul	2004	Biotropica	Sex in space: Pollination among spatially isolated plants	N			NA	NA	NA	Y
Henriquez	2004	Revista Chilena De Historia Natural	Effects of habitat fragmentation on seed quality of Lapageria rosea	Y	disturbed/ undisturbed	seed set	Y	N	none	N

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Hooftman	2004	Conservation Biology	Genetic effects of habitat fragmentation on common species of Swiss fen meadows	Y	patch size	genetic diversity	Y	N	none	N
Johnson	2004	Biotropica	Factors contributing to variation in seed production among remnant populations of the endangered daisy Gerbera aurantiaca	N	patch size	seed set	Y	N	none	N
Johnson	2004	Biological Conservation	Fruiting failure and limited recruitment in remnant populations of the hawkmoth-pollinated tree Oxyanthus pyriformis subsp pyriformis (Rubiaceae)	N	habitat loss	pollination	Y	N	none	N
Klein	2004	Journal of Animal Ecology	Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems	N	disturbed/ undisturbed	pollinator movement, pollinator abundance/diversity	N	N	none	N
Kreyer	2004	Biological Conservation	Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with Bombus terrestris agg. and Bombus pascuorum (Hymenoptera, Apidae)	N	matrix quality	pollinator movement	Y	N	none	N
Murphy	2004	Oikos	Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter?	N			NA	NA	NA	Y
Odat	2004	Molecular Ecology	Genetic diversity of Ranunculus acris L. (Ranunculaceae) populations in relation to species diversity and habitat type in grassland communities	N	disturbed/ undisturbed	genetic diversity	N	N	none	N
Quesada	2004	Biotropica	Effects of forest fragmentation on pollinator activity and consequences for plant reproductive success and mating patterns in bat-pollinated bombacaceous trees	Y	disturbed/ undisturbed	visitation rates, seed set	Y	N	none	N
Ricketts	2004	Conservation Biology	Tropical forest fragments enhance pollinator activity in nearby coffee crops	N			NA	NA	NA	Y
Samejima	2004	Biological Conservation	The effects of human disturbance on a stingless bee community in a tropical rainforest	N	disturbed/ undisturbed	pollinator abundance/diversity	N	N	none	N
Somanathan	2004	Biotropica	Does Neighborhood floral display matter? Fruit set in carpenter bee-pollinated Heterophragma quadriloculare and beetle-pollinated Lasiosiphon eriocephalus	N	isolation	seed set	N	N	none	N
Waites	2004	Journal of Ecology	Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in Lythrum salicaria	N	patch size	seed set, visitation rates, pollination	Y	N	none	N
Yates	2004	Austral Ecology	Breeding system, pollination and demography in the rare granite endemic shrub Verticordia staminosa ssp staminosa in south-west Western Australia	N	patch size	visitation rates, seed set	Y	N	none	N
Bernard	2003	Biotropica	Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil	N	disturbed/ undisturbed	pollinator movement	Y	N	none	N
Bhattacharya	2003	Biological Conservation	Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area?	N	matrix quality	pollinator movement	Y	N	none	N
Culley	2003	Molecular Ecology	Genetic effects of habitat fragmentation in Viola pubescens (Violaceae), a perennial herb with chasmogamous and cleistogamous flowers	Y	patch size, isolation	genetic diversity	Y	N	none	N
Dick	2003	Molecular Ecology	Pollen dispersal of tropical trees (Dinizia excelsa: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest	N	disturbed/ undisturbed	pollen movement	Y	N	none	N
Ehrlen	2003	Journal of Ecology	Large-scale spatial dynamics of plants: a response to Freckleton & Watkinson	N			NA	NA	NA	Y
Forsyth	2003	Oecologia	Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect	N	isolation	seed set	N	N	none	N

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Fuchs	2003	Conservation Biology	Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree Pachira quinata	Y	isolation, matrix quality	genetic diversity	Y	N	none	N
Haddad	2003	Ecology	Corridor use by diverse taxa	N	corridors	pollinator movement	Y	N	none	N
Hirsch	2003	Agriculture Ecosystems & Environment	The influence of matrix type on flower visitors of Centaurea jacea L	N	matrix quality	visitation rates	N	N	none	N
Ishihama	2003	Functional Ecology	Seed set and gene flow patterns in an experimental population of an endangered heterostylous herb with controlled local opposite-morph density	N	isolation	seed set	N	N	none	N
Jules	2003	Journal of Vegetation Science	A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought	Y			NA	NA	NA	Y
Klein	2003	Journal of Applied Ecology	Pollination of Coffea canephora in relation to local and regional agroforestry management	N	isolation	pollination	Y	N	none	N
Knight	2003	Oecologia	Floral density, pollen limitation, and reproductive success in Trillium grandiflorum	N	isolation	genetic diversity	Y	N	none	N
Koenig	2003	Trends in Ecology & Evolution	Is pollen limited? The answer is blowin' in the wind	N			NA	NA	NA	Y
Lopez-Pujol	2003	Plant Biology	Effects of habitat fragmentation on allozyme diversity and conservation status of the coastal sand dune plant Stachys maritima (Lamiaceae) in the Iberian Peninsula	Y	habitat loss	genetic diversity	Y	N	none	N
Murren	2003	Journal of Evolutionary Biology	Spatial and demographic population genetic structure in Catasetum viridiflavum across a human-disturbed habitat	N	patch size, isolation	genetic diversity	Y	N	none	N
Osada	2003	Ecological Research	Community-level flowering phenology and fruit set: Comparative study of 25 woody species in a secondary forest in Japan	N	habitat quality	seed set	Y	N	none	N
Potts	2003	Ecology	Linking bees and flowers: How do floral communities structure pollinator communities?	N	habitat quality	pollinator abundance/diversity	N	N	none	N
Quesada	2003	Oecologia	Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera : Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree Ceiba grandiflora	N	disturbed/ undisturbed	pollination, seed set, visitation rates	Y	N	none	N
Severns	2003	Biological Conservation	Inbreeding and small population size reduce seed set in a threatened and fragmented plant species, Lupinus sulphureus ssp kincaidii (Fabaceae)	N	patch size	seed set	Y	N	none	N
Smith-Ramirez	2003	Austral Ecology	Foraging behaviour of bird pollinators on Embothrium coccineum (Proteaceae) trees in forest fragments and pastures in southern Chile	N	patch size	visitation rates	Y	N	none	N
Wratten	2003	Oecologia	Field boundaries as barriers to movement of hover flies (Diptera : Syrphidae) in cultivated land	N	edge	pollinator movement	N	N	none	N
Aizen	2002	Journal of Vegetation Science	Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter?	N			NA	NA	NA	Y
Aizen	2002	Revista Chilena De Historia Natural	Natural history and conservation of plant-animal mutualisms in the temperate forest of southern South America	N			NA	NA	NA	Y
Bruna	2002	Conservation Biology	Habitat fragmentation and the demographic structure of an Amazonian understory herb (Heliconia acuminata)	Y	patch size	genetic diversity	Y	N	none	N

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Cascante	2002	Conservation Biology	Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree Samanea saman	Y	patch size, isolation	pollination, pollinator abundance/diversity	Y	N	none	N
Donaldson	2002	Conservation Biology	Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa	Y	patch size, isolation	pollination, pollinator abundance/diversity	Y	N	none	N
Dupre	2002	Journal of Ecology	Habitat configuration, species traits and plant distributions	N			NA	NA	NA	Y
Eltz	2002	Oecologia	Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia	N	edge	pollinator movement	N	N	none	N
Goverde	2002	Biological Conservation	Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee Bombus veteranus on calcareous grasslands	Y	patch size	pollinator movement	Y	N	none	N
Jacquemyn	2002	Oecologia	Patch occupancy, population size and reproductive success of a forest herb (Primula elatior) in a fragmented landscape	N	patch size	seed set	Y	N	none	N
Klein	2002	Conservation Biology	Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps	N	habitat quality	pollinator abundance/diversity	Y	N	none	N
Leimu	2002	Oikos	Effects of population size, seed predation and plant size on male and female reproductive success in Vincetoxicum hirundinaria (Asclepiadaceae)	N	patch size	seed set	N	N	none	N
Lennartsson	2002	Ecology	Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations	N	habitat loss	pollination	Y	N	none	N
Lofgren	2002	Ecoscience	Effects of isolation on distribution, fecundity, and survival in the self-incompatible Achillea millefolium (L.)	N	patch size, isolation	seed set	N	N	none	N
Murren	2002	Journal of Ecology	Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success	Y	disturbed/ undisturbed	pollinator abundance/diversity	Y	N	none	N
Sork	2002	Molecular Ecology	Pollen movement in declining populations of California Valley oak, Quercus lobata: where have all the fathers gone?	N			NA	NA	NA	Y
Steffan-Dewenter	2002	Ecology	Scale-dependent effects of landscape context on three pollinator guilds	N	habitat loss	pollinator abundance/diversity	Y	N	none	N
Steffan-Dewenter	2002	Biological Conservation	Insect communities and biotic interactions on fragmented calcareous grasslands - a mini review	N			NA	NA	NA	Y
Stoner	2002	Biotropica	Effects of forest fragmentation on the Colima long-nosed bat (Musonycteris harrisoni) foraging in tropical dry forest of Jalisco, Mexico	Y	disturbed/ undisturbed	pollinator movement	Y	N	none	N
Tomimatsu	2002	Conservation Biology	Effects of forest fragmentation on seed production of the understory herb Trillium camschatcense	Y	disturbed/ undisturbed	seed set	Y	N	none	N
Tscharntke	2002	Ecological Applications	Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes	N	habitat loss	pollinator abundance/diversity	Y	N	none	N
Van Rossum	2002	Conservation Biology	Commonness and long-term survival in fragmented habitats: Primula elatior as a study case	N	patch size, isolation	genetic diversity	Y	N	none	N
Borgella	2001	Biotropica	Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica	N	patch size	pollinator abundance/diversity, pollinator diet shift	Y	N	none	N

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Cane	2001	Conservation Ecology	Habitat fragmentation and native bees: a premature verdict?	Y			NA	NA	NA	Y
Cane	2001	Conservation Ecology	Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences	N			NA	NA	NA	Y
Costin	2001	Biological Conservation	Reproductive success does not decline in fragmented populations of Leucochrysum albicans subsp albicans var. tricolor (Asteraceae)	N	habitat loss	pollination	Y	N	none	N
Cruzan	2001	Evolution	Population size and fragmentation thresholds for the maintenance of genetic diversity in the herbaceous endemic Scutellaria montana (Lamiaceae)	Y			NA	NA	NA	Y
Ghazoul	2001	Plant Ecology	Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica	N	habitat quality, isolation	pollination	Y	N	none	N
Gonzalez-Astorga	2001	Evolutionary Ecology Research	Effect of habitat fragmentation on the genetic structure of the narrow endemic Brongniartia vazquezii	Y	habitat loss	genetic diversity	Y	N	none	N
Groom	2001	Biological Conservation	Consequences of subpopulation isolation for pollination, herbivory, and population growth in Clarkia concinna concinna (Onagraceae)	N	isolation	pollination	N	N	none	N
Gross	2001	Biological Conservation	The effect of introduced honeybees on native bee visitation and fruit-set in Dillwynia juniperina (Fabaceae) in a fragmented ecosystem	N	habitat quality	visitation rates	Y	N	none	N
Hackney	2001	Conservation Biology	Experimental demonstration of an Allee effect in American ginseng	N	patch size	seed set	N	N	none	N
Kelly	2001	Ecology	Evaluating the wind pollination benefits of mast seeding	N	isolation	pollination	Y	N	none	N
Kery	2001	Journal of Ecology	The effect of plant population size on the interactions between the rare plant Gentiana cruciata and its specialized herbivore Maculinea rebeli	N	patch size	seed set	Y	N	none	N
Knapp	2001	Oecologia	Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations	N	isolation	pollination	Y	N	none	N
Lindberg	2001	Journal of Tropical Ecology	The fragility of extreme specialization: Passiflora mixta and its pollinating hummingbird Ensifera ensifera	N	disturbed/ undisturbed	pollination	N	N	none	N
Malo	2001	Biotropica	Population fragmentation, florivory, and the effects of flower morphology alterations on the pollination success of Myrmecophila tibicinis (Orchidaceae)	Y	patch size	pollination	Y	N	none	N
Mavraganis	2001	Oikos	Effects of population size and isolation on reproductive output in Aquilegia canadensis (Ranunculaceae)	N	patch size, isolation	seed set	Y	N	none	N
Mustajarvi	2001	Journal of Ecology	Consequences of plant population size and density for plant-pollinator interactions and plant performance	N	patch size, isolation	pollination	Y	N	none	N
Osborne	2001	Agriculture Ecosystems & Environment	Site constancy of bumble bees in an experimentally patchy habitat	N	patch size	visitation rates	N	N	none	N
Packer	2001	Conservation Ecology	Population genetic aspects of pollinator decline	N			NA	NA	NA	Y
Schulke	2001	Oecologia	Long-distance pollinator flights and pollen dispersal between populations of Delphinium nuttallianum	N	isolation	pollen movement, pollinator movement	Y	N	none	N
Spira	2001	Natural Areas Journal	Plant-pollinator interactions: A threatened mutualism with implications for the ecology and management of rare plants	N			NA	NA	NA	Y
Washitani	2001	Population Ecology	Plant conservation ecology for management and restoration of riparian habitats of lowland Japan	N			NA	NA	NA	Y

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First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Wolf	2001	Conservation Biology	Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory	N	patch size	pollination	Y	N	none	N
Adler	2000	Biotropica	Reproductive phenology of a tropical canopy tree, Spondias mombin	N	patch size, isolation	pollination	N	N	none	N
Craig	2000	Annual Review of Ecology and Systematics	Conservation issues in New Zealand	N			NA	NA	NA	Y
Cunningham	2000	Conservation Biology	Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland	Y	habitat loss	pollination	Y	N	none	N
Hendrix	2000	Conservation Biology	Population size and reproduction in Phlox pilosa	N	patch size	seed set	Y	N	none	N
Jaeger	2000	Landscape Ecology	Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation	Y			NA	NA	NA	Y
Kery	2000	Journal of Ecology	Reduced fecundity and offspring performance in small populations of the declining grassland plants Primula veris and Gentiana lutea	N	patch size	seed set	N	N	none	N
Matsumura	2000	Ecological Research	Effects of population size and pollinator limitation on seed-set of Primula sieboldii populations in a fragmented landscape	N	patch size	visitation rates, seed set	Y	N	none	N
Nielsen	2000	Ecoscience	Bumble bee pollination of the sticky catchfly in a fragmented agricultural landscape	N	patch size, isolation	pollination	Y	N	none	N
Parra-Tabla	2000	Biological Conservation	Female and male pollination success of Oncidium ascendens Lindey (Orchidaceae) in two contrasting habitat patches: forest vs agricultural field	N	disturbed/ undisturbed	pollination	N	N	none	N
Roubik	2000	Conservation Biology	Pollination system stability in tropical America	N			NA	NA	NA	Y
Somanathan	2000	Biological Conservation	Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India	N	disturbed/ undisturbed	pollination	Y	N	none	N
Van der Merwe	2000	Molecular Ecology	Spatial and temporal aspects of the genetic structure of Juniperus communis populations	N	habitat loss	genetic diversity	N	N	none	N
Warburton	2000	Biological Conservation	Clonality and sexual reproductive failure in remnant populations of Santalum lanceolatum (Santalaceae)	N	isolation	seed set	Y	N	none	N
Wolf	2000	Conservation Biology	Influence of habitat patchiness on genetic diversity and spatial structure of a serpentine endemic plant	N	patch size, isolation	genetic diversity	Y	N	none	N
Bigger	1999	Natural Areas Journal	Consequences of patch size and isolation for a rare plant: Pollen limitation and seed predation	N	patch size, isolation	pollination	N	N	none	N
Ferdy	1999	Oikos	Pollinator-induced density dependence in deceptive species	N	patch size, isolation	visitation rates	N	N	none	N
Gigord	1999	Biological Conservation	Effects of habitat fragmentation on Dombeya acutangula (Sterculiaceae), a native tree on La Reunion (Indian Ocean)	Y	patch size	pollination	Y	N	none	N
Jules	1999	Conservation Biology	Mechanisms of reduced Trillium recruitment along edges of old-growth forest fragments	N	edge	pollination	Y	N	none	N
Kappelle	1999	Biodiversity and Conservation	Effects of climate change on biodiversity: a review and identification of key research issues	N			NA	NA	NA	Y
Law	1999	Biological Conservation	Common blossom bats (Syconycteris australis) as pollinators in fragmented Australian tropical rainforest	N			NA	NA	NA	Y
Osborne	1999	Journal of Applied Ecology	A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar	N			NA	NA	NA	Y

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Ouborg	1999	Journal of Ecology	Population genetics, molecular markers and the study of dispersal in plants	N			NA	NA	NA	Y
Robertson	1999	Conservation Biology	Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae)	N	habitat quality	pollination	N	N	none	N
Santos	1999	Ecography	Dispersal of Spanish juniper Juniperus thurifera by birds and mammals in a fragmented landscape	N	patch size	seed set	Y	N	none	N
Sork	1999	Trends in Ecology & Evolution	Landscape approaches to historical and contemporary gene flow in plants	N			NA	NA	NA	Y
Steffan-Dewenter	1999	Oecologia	Effects of habitat isolation on pollinator communities and seed set	N	isolation	seed set	Y	N	none	N
Traveset	1999	Revista Chilena De Historia Natural	The importance of mutualisms for biodiversity conservation in insular ecosystems	N			NA	NA	NA	Y
Allen-Wardell	1998	Conservation Biology	The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields	N			NA	NA	NA	Y
Benitez-Malvido	1998	Conservation Biology	Impact of forest fragmentation on seedling abundance in a tropical rain forest	Y	patch size	seed set	Y	N	none	N
Berge	1998	Oikos	The effect of breeding systems and pollination vectors on the genetic variation of small plant populations within an agricultural landscape	N	patch size	genetic diversity	Y	N	none	N
Bustamante	1998	Biodiversity and Conservation	The decline of an endangered temperate ecosystem: the ruil (Nothofagus alessandrii) forest in central Chile	N	habitat loss	pollination syndrome	Y	N	none	N
Ghazoul	1998	Journal of Ecology	Disturbance-induced density-dependent seed set in Shorea siamensis (Dipterocarpaceae), a tropical forest tree	N	disturbed/ undisturbed	pollination	N	N	none	N
Groom	1998	American Naturalist	Allee effects limit population viability of an annual plant	N	patch size	pollination	Y	N	none	N
James	1998	Biotropica	Mating systems of three tropical dry forest tree species	N	habitat quality	genetic diversity	Y	N	none	N
Kearns	1998	Annual Review of Ecology and Systematics	Endangered mutualisms: The conservation of plant-pollinator interactions	N			NA	NA	NA	Y
Lundberg	1998	Theoretical Population Biology	Population dynamics of resource limited plants and their pollinators	N			NA	NA	NA	Y
Mawdsley	1998	Conservation Biology	Population persistence, pollination mutualisms, and figs in fragmented tropical landscapes	N	patch size	pollination	Y	N	none	N
Oostermeijer	1998	Conservation Biology	Relationships between population and habitat characteristics and reproduction of the rare Gentiana pneumonanthe L	N	patch size, habitat quality	seed set	Y	N	none	N
Shapcott	1998	Molecular Ecology	The patterns of genetic diversity in Carpentaria acuminata (Arecaceae), and rainforest history in northern Australia	N	patch size	genetic diversity	N	N	none	N
Shapcott	1998	Journal of Tropical Ecology	Vagile but inbred: patterns of inbreeding and the genetic structure within populations of the monsoon rain forest tree Syzygium nervosum (Myrtaceae) in northern Australia	N	isolation	genetic diversity	Y	N	none	N
Tscharntke	1998	Journal of Applied Ecology	Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions	N	habitat quality	pollinator abundance/diversity	Y	N	none	N
Dawson	1997	Molecular Ecology	Simple sequence repeats provide a direct estimate of pollen-mediated gene dispersal in the tropical tree Gliricidia sepium	N	isolation	genetic diversity	N	N	none	N

APPENDIX A. (Continued)

First author	Date	Journal	Title	FT	Landscape metric	Response variable	Discuss	Separate	Separation technique	Review
Kunin	1997	Journal of Ecology	Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of Brassica kaber	N			NA	NA	NA	Y
Malanson	1997	Plant Ecology	Effects of dispersal, population delays, and forest fragmentation on tree migration rates	Y			NA	NA	NA	Y
Roll	1997	Conservation Biology	Reproductive success increases with local density of conspecifics in a desert mustard (Lesquerella fendleri)	N	isolation	pollination	Y	N	none	N
Agren	1996	Ecology	Population size, pollinator limitation, and seed set in the self-incompatible herb Lythrum salicaria	N	patch size	pollination	Y	N	none	N
Alexandersson	1996	Oecologia	Population size, pollinator visitation and fruit production in the deceptive orchid Calypso bulbosa	N	patch size	seed set, visitation rates	N	N	none	N
Didham	1996	Trends in Ecology & Evolution	Insects in fragmented forests: A functional approach	N			NA	NA	NA	Y
Washitani	1996	Conservation Biology	Predicted genetic consequences of strong fertility selection due to pollinator loss in an isolated population of Primula sieboldii	N	isolation	pollination, visitation rates	N	N	none	N
Aizen	1994	Ecological Applications	Habitat Fragmentation, Native Insect Pollinators, and Feral Honey-Bees in Argentine Chaco Serrano	Y	patch size	visitation rates	Y	N	none	N
Aizen	1994	Ecology	Forest Fragmentation, Pollination, and Plant Reproduction in a Chaco Dry Forest, Argentina	Y	patch size	pollination, seed set	Y	N	none	N
Westerbergh	1994	Oikos	Gene Flow and Pollinator Behavior in Silene-Dioica Populations	N	matrix quality	genetic diversity	Y	N	none	N
Willson	1994	Conservation Biology	Avian Communities of Fragmented South-Temperate Rain-Forests in Chile	N	patch size	pollinator abundance/diversity	Y	N	none	N
Armbruster	1993	Evolution	Evolution of Plant Pollination Systems - Hypotheses and Tests with the Neotropical Vine Dalechampia	N			NA	NA	NA	Y
Law	1993	Wildlife Research	Roosting and Foraging Ecology of the Queensland Blossom Bat (Syconycteris-Australis) in North-Eastern New-South-Wales - Flexibility in Response to Seasonal-Variation	N	disturbed/ undisturbed	pollinator movement	N	N	none	N
Rasmussen	1992	Oecologia	Gene Flow Inferred from Seed Dispersal and Pollinator Behavior Compared to DNA Analysis of Restriction Site Variation in a Patchy Population of Lotus-Corniculatus L	N	isolation	pollinator movement	N	N	none	N

APPENDIX B. Predictive contribution of environmental layers used to generate the *H. tortuosa* habitat suitability model. Landsat 2003 bands are indicated by 'l03' followed by the band (b) number. Variable definitions are as follows: elevation = elevation in meters, forest = forest/non-forest, edge = distance to the nearest edge in meters, aspect = aspect in degrees, stream = distance to the nearest stream in meters, slope = slope in degrees.

Variable	Percent contribution	Permutation importance
elevation	54.1	58.3
forest	22	17.6
edge	4.5	9.4
l03_b62	4	2.3
l03_b10	3.5	1.1
aspect	2.7	0.6
l03_b502	2.3	1.8
l03_b80	1.3	1.3
stream	1.3	1.9
slope	1.2	0.1
l03_b40	0.8	0.4
l03_b30	0.6	2
l03_b61	0.6	0.2
l03_b70	0.6	1.5
l03_b20	0.4	1.4